
Volume 78
Number 4
1991

Annals
of the
Missouri
Botanical
Garden



MONOGRAPH OF THE
NEOTROPICAL FERN GENUS
STIGMATOPTERIS
(DRYOPTERIDACEAE)¹

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ABSTRACT

Stigmatopteris contains 24 species with no varieties or subspecies. It is distinguished from all other genera of Dryopteridaceae (sensu stricto) by numerous punctate glands in the lamina, scales with uniseriate teeth or cilia, glandular cells terminating the apices of the teeth or cilia, and clavate vein apices that end behind the leaf margin. Other characteristics shared by all or nearly all species of the genus but also found in other dryopteroid ferns are nonindusiate sori, thin-textured leaves, glabrous laminar tissue, acuminate-serrate pinna, apices, thin, flaccid, tan or orangish scales, erect or short-creeping stems, and minutely pubescent adaxial grooves of the axes. Within the Dryopteridaceae, *Stigmatopteris* forms a clade with *Cyclodium*, *Olfersia*, and *Polybotrya*, held together by the synapomorphy of pubescent adaxial grooves of the axes. The genus is entirely neotropical and primarily montane, ranging from the Antilles and southern Mexico to southern Brazil but conspicuously absent from most of the Amazon basin. The Andes are the center of diversity for the genus, harboring eleven species, two of which are endemic. The coastal mountains of southeastern Brazil are another center, with six species, all of which are endemic. The Greater Antilles have also been important in the diversification of *Stigmatopteris* because they contain three species, all of which are endemic. All members of the genus grow in wet forests, generally from 200 to 2,000 m.

RESUMEN

Stigmatopteris contiene 24 especies sin subespecies ni variedades. Es distinguido de todos los otros géneros de las dryopteridáceas (sensu stricto) por las numerosas glándulas punctatas, escamas con dientes o cilia numerosas, células glandulares terminando los ápices de los dientes o cilia, y ápices clavatas de las venas que terminan atrás del margen de la lámina. Otras características compartidas por todas o casi todas las especies en el género, pero encontrado

¹ I thank Alan R. Smith (UC) for helpful discussions on all aspects of this work and Robert G. Stolze (F) for first pointing out to me that *Stigmatopteris* needed a modern monograph. Rolla M. Tryon (then at GH, now at USF) reviewed the nomenclatural parts of the species treatments and suggested improvements. Jorge V. Crisci (LP) provided assistance in running the HENNIG86 program used in the cladistic analysis of the species, and Enrique Forero (MO) and Warren D. Stevens (MO) facilitated funding for annotation labels and scanning electron microscopy. Gerrit Davidse (MO) and Henk van der Werff (MO) also provided support and encouragement for this project. I thank the curators of the following herbaria for making their specimens available for study: AAU, B, BM, CM, COL, CR, DUKE, F, G, GH, K, L, LIL, MICH, MU, NY, P, PH, PORT, QCNE, SI, UC, US, VEN, Z.

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también en otros helechos dryopteroides, son los soros no indusiados, hojas membranáceas, tejido de la lámina glabro, ápices de las pinnas acuminadas-seratas, escamas membranáceas, flácidas, pardas claras o naranjizas, rizomas rectos o corte-reptantes, y los surcos adaxiales de la lámina cortamente pubescentes adentro. En las dryopteridaceas, *Stigmatopteris* hace un grupo monofilético con *Cyclodium*, *Olfersia*, y *Polybotrya*, basado en la sinapomorfía de surcos adaxiales pubescentes. El género es completamente neotropical y principalmente en regiones montañosas con bosques, extendiéndose desde las Antillas y sur de México hasta el sur de Brasil pero ausente de la mayoría de la cuenca Amazónica. Los Andes son el centro de diversidad para el género, con once especies, dos de las cuales son endémicas. Las montañas costales del sureste de Brasil son otro centro, con seis especies, todas las cuales son endémicas. Las Antillas han sido importante también en la diversificación de *Stigmatopteris*, con tres especies, todas de las cuales son endémicas. Todas las especies en el género existen en bosques húmedos, generalmente de 200 a 2,000 m.

TAXONOMIC HISTORY

Stigmatopteris was first proposed by Christensen in 1909. Until then, all of its species had been placed in *Dryopteris*, a genus that comprised a vast, unrelated assemblage of nearly 1,000 species. Four years later, in the first volume of his *Dryopteris* monograph, Christensen (1913) changed his mind about the rank of *Stigmatopteris*, placing it back in *Dryopteris* as a subgenus, but with the proviso that it could be treated, along with most of his other subgenera, as a distinct genus. Nowadays, pteridologists follow Christensen's original placement, giving *Stigmatopteris* full generic status.

Christensen's (1913) *Dryopteris* monograph also widened the definition of *Stigmatopteris* by including three species in what he informally called the "*Peltochlaena* group," which differed from true *Stigmatopteris* by having an indusium and a thick, nonglandular lamina. This group is now considered part of a separate genus, *Cyclodium*, which was recently monographed by Smith (1986). The species of *Cyclodium* previously placed in *Stigmatopteris* are listed in the excluded taxa section.

GEOGRAPHY

Stigmatopteris is entirely neotropical, extending from the Antilles and the state of Veracruz, Mexico, southward to southeastern Brazil (Fig. 1). The genus is absent from the Amazon basin except along the western portion adjacent to the Andes. It is primarily a montane genus, occurring in wet forests from 200 to 2,000 m, with the highest elevation being 2,500 m recorded for *S. rotundata* in Panama.

Species diversity and endemism in *Stigmatopteris* can be conveniently discussed using the regional centers of high endemism and species richness delimited by Tryon (1972) for tropical American ferns (Fig. 2). The region of highest

diversity and endemism for the genus is the Andes, containing eleven species and two endemics (*S. ichthiosma*, and *S. pellucidopunctata*). Two species (*S. bulbifera* and *S. pterorachis*) are near-endemics, as they also occur outside the Andean Region in the Santa Marta Mountains of northern Colombia. Within the Andean Region, Colombia and Ecuador have more species (ten) than any other country (Tables 1, 2).

The coastal mountains of northern Venezuela have two species of *Stigmatopteris*, one of which is endemic (*S. nephrodioides*). Although these mountains do not harbor a large number of species, they could be considered a secondary regional center in Tryon's scheme because they have many endemic species.

The region with the next highest number of species is Central American, with seven species, one of which is endemic (*S. contracta*). With the exception of *S. contracta*, all of the other species extend southward into the Andean Region, giving the two regions a high floristic affinity.

Southeastern Brazil has played a major role in the diversification of *Stigmatopteris* because it has six species, all of which are endemic. The Greater Antilles have also been important, having three species, all of which are endemic.

The Guianan and Mexican centers contain few species and thus have not been important in the diversification of *Stigmatopteris*. The Mexican Region boasts one endemic (*S. chimalapensis*), but it is known only from one collection and may eventually be found outside of the region.

MORPHOLOGY

Internal glands in the lamina. The glands can usually be seen with a dissecting microscope and, in oblique light, they appear as tiny raised bumps on the leaf surface (Fig. 3a, c). They often dry blackish. Perhaps the best way to see the glands



FIGURE 1. Distribution of *Stigmatopteris*.

is to look through a hand lens with the lamina illuminated from behind. Viewed this way, the glands appear as pellucid dots in the lamina (Fig. 3b). The glands are more conspicuous in some species than in others. Occasionally, they are so large and abundant that they are visible to the naked eye, but in *S. opaca*, a species with a thick lamina, the glands are not visible. The genus is named for these glands: from the Greek *stigmatos*, punctate, and *pterus*, fern.

Other genera of dryopteroid ferns also have internal glands, but these are extremely small and visible only by thin-sectioning and viewing under a compound microscope (Widén et al., 1983). The large glands in *Stigmatopteris* are probably homologous with these smaller ones, but nothing is known about the glands' structure, development, chemical contents, or role in metabolism.

Scales. The scale characteristic that distin-

guishes *Stigmatopteris* from all other genera of dryopteroid ferns is the presence of uniseriate cilia that end in a bulbous, often orange or brownish, glandular cell (Fig. 4). In other dryopteroid ferns, marginal teeth or processes are formed by the projecting end walls of two adjacent cells (Moran, 1987, fig. 7) and are never uniseriate or terminated by a glandular cell.

The scales of *Stigmatopteris* are more uniform than those in other genera of dryopteroid ferns. Although the shape differs, all species of *Stigmatopteris* have scales that are thin, flaccid, and tan or light orangish.

The scales decrease in size from the proximal to distal portions of the lamina until they become uniseriate or only 2–3 cells wide at the base (Figs. 4, 12b). These highly reduced scales, termed "proscapes" or "microscales," are present on all species of the genus, and a dissecting microscope

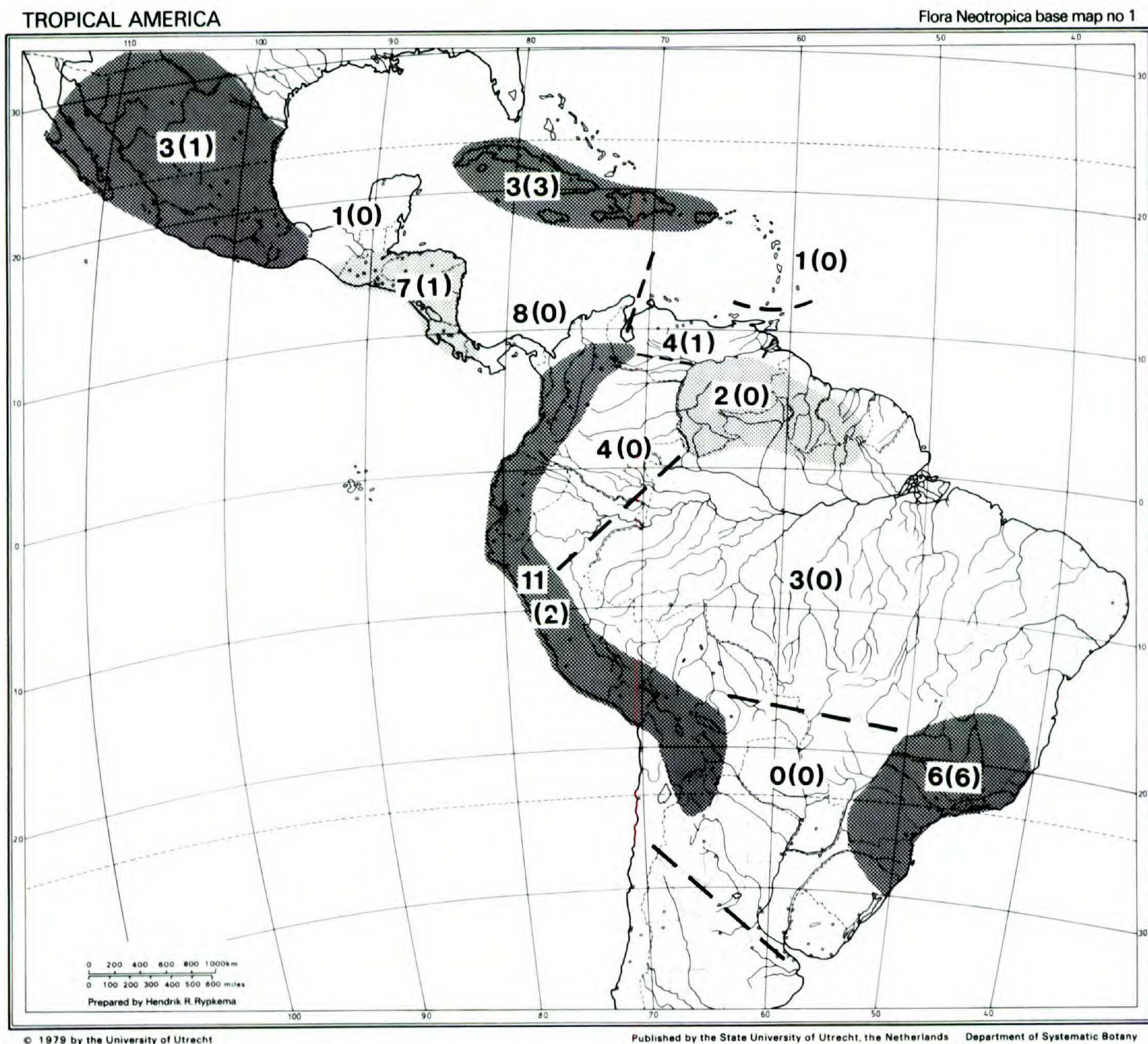


FIGURE 2. Distribution of *Stigmatopteris* species within regional centers of diversity and endemism for tropical American ferns defined by Tryon (1972). Primary centers are indicated with dark shading, secondary centers with light shading. The number on the left is the total number of species, and the number in parentheses indicates how many of those species are endemic.

is needed to see them. Their lateral processes are usually terminated by glandular cells.

Veins. Unlike most dryopteroid ferns, the veins of *Stigmatopteris* end behind the margin in clavate apices which are best seen adaxially (Fig. 23a). All other genera of dryopteroid ferns (*sensu stricto*) have the veins ending at or close to the margin, and the apices are slender, not thickened.

Indusia. *Stigmatopteris* is nonindusiate. Three species have an indusiumlike scale associated with the sorus (Figs. 17b, 18a), but these scales are certainly not homologous with the large, firm, thick-textured, circular indusia found in the outgroup genus *Cyclodium*. Although independently derived in *Stigmatopteris*, the lack of an indusium is not unique because many other dryopteroid ferns also lack an indusium.

Lamina shape and texture. All species have

pinnae with long-acuminate apices that are serrate to the tip. The pinnae are equilaterally symmetrical, but some of the large species such as *S. contracta* and *S. lechleri* may have basal pinnae that are elongated basiscopically. The texture of the lamina is thin and papyraceous, except for that of *S. opaca*, which is thick and slightly chartaceous.

Hairs. All species of *Stigmatopteris* lack hairs except in the adaxial grooves of the rachis and costae. These hairs are 0.05–0.2 mm long, 1- or 2-celled, unbranched, and colorless to reddish. They are also found in the same position in *Cyclodium*, *Olfersia*, and *Polybotrya* and are a synapomorphy that holds these three genera and *Stigmatopteris* on the same clade within the Dryopteridaceae (see evolutionary relationships section). *Stigmatopteris heterophlebia* and *S. bulbifera*, however, are ex-

TABLE 1. Distribution of *Stigmatopteris* by country. Endemics are in boldface.

Mexico: 3 species, 1 endemic. **chimalapensis**, longicaudata, sordida.
 Guatemala: 2 species, no endemics. longicaudata, sordida.
 Honduras: 1 species, not endemic. longicaudata.
 Nicaragua: 2 species, no endemics. heterophlebia, sordida.
 Costa Rica: 5 species, no endemics. contracta, heterophlebia, killipiana, longicaudata, sordida.
 Panama: 6 species, no endemics. contracta, heterophlebia, killipiana, longicaudata, michaelis, sordida.
 Cuba: 1 species, 1 endemic. **hemiptera**.
 Jamaica: 2 species, 1 endemic. gemmipara, **jamaicensis**.
 Haiti: 1 species, not endemic. gemmipara.
 Guadeloupe: 1 species, not endemic. rotundata.
 Dominica: 1 species, not endemic. rotundata.
 Martinique: 1 species, not endemic. rotundata.
 St. Lucia: 1 species, not endemic. rotundata.
 St. Vincent: 1 species, not endemic. rotundata.
 Grenada: 1 species, not endemic. rotundata.
 Trinidad: 1 species, not endemic. rotundata.
 French Guiana: 1 species, not endemic. rotundata.
 Guyana: 1 species, not endemic. longicaudata.
 Venezuela: 5 species, 1 endemic. lechleri, longicaudata, **nephrodioides**, pterorhachis, rotundata.
 Colombia: 10 species, no endemics. bulbifera, heterophlebia, ichthiosma, killipiana, lechleri, longicaudata, michaelis, pterorhachis, pellucidopunctata, sordida.
 Ecuador: 10 species, no endemics. bulbifera, heterophlebia, ichthiosma, killipiana, lechleri, longicaudata, michaelis, opaca, pterorhachis, pellucidopunctata, sordida.
 Peru: 5 species, no endemics. heterophlebia, lechleri, longicaudata, opaca, pellucidopunctata.
 Bolivia: 2 species, no endemics. longicaudata, pellucidopunctata.
 Brazil (southeastern): 6 species, 6 endemics. **brevinervis**, **caudata**, **heterocarpa**, **prionites**, **tyucana**, **ulei**.

TABLE 2. The species of *Stigmatopteris* and their distribution by country.

1. *S. brevinervis* (Fée) R. C. Moran: southeastern Brazil.
2. *S. bulbifera* R. C. Moran: Colombia, Ecuador.
3. *S. caudata* (Raddi) C. Chr.: southeastern Brazil.
4. *S. chimalapensis* Mickel & Beitel: southern Mexico.
5. *S. contracta* (Christ) C. Chr.: Costa Rica, Panama.
6. *S. gemmipara* C. Chr.: Jamaica, Haiti.
7. *S. hemiptera* (Maxon) C. Chr.: Cuba.
8. *S. heterocarpa* (Fée) Rosenstock: southeastern Brazil.
9. *S. heterophlebia* (Baker) R. C. Moran: Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru.
10. *S. ichthiosma* (Sodirol) C. Chr.: western Ecuador.
11. *S. jamaicensis* (Desv.) Proctor: Jamaica.
12. *S. killipiana* Lellinger: Costa Rica, Panama, Colombia, Ecuador.
13. *S. lechleri* (Mett.) C. Chr.: Costa Rica, Venezuela, Colombia, Ecuador, Peru.
14. *S. longicaudata* (Liebm.) C. Chr.: Mexico, Guatemala, Honduras, Costa Rica, Panama, French Guiana, Venezuela, Colombia, Ecuador, Peru, Bolivia.
15. *S. michaelis* (Baker) C. Chr.: Panama, Colombia, Ecuador.
16. *S. nephrodioides* (Klotzsch) C. Chr.: Venezuela.
17. *S. opaca* (Baker) C. Chr.: Ecuador, Peru.
18. *S. pellucidopunctata* (C. Chr.) C. Chr.: Colombia, Ecuador, Peru, Bolivia.
19. *S. prionites* (Kunze) C. Chr.: southeastern Brazil.
20. *S. pterorhachis* R. C. Moran: Venezuela, Colombia.
21. *S. rotundata* (Willd.) C. Chr.: Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, Grenada, Trinidad, French Guiana, Guyana, Venezuela.
22. *S. sordida* (Maxon) C. Chr.: Mexico, Guatemala, Nicaragua, Costa Rica, Panama, Colombia, Ecuador.
23. *S. tyucana* (Raddi) C. Chr.: southeastern Brazil.
24. *S. ulei* (Christ) Sehnem: southeastern Brazil.

ceptions to the general condition of hairlessness in the genus because their axes are covered abaxially with capitate-glandular hairs.

Sporangia. The sporangia are like those described by Moran (1987) for *Polybotrya*, except that the stalks lack a hairlike paraphysis.

Petiole anatomy. A cross section of the petiole shows that the vascular bundles are arranged in a mushroomlike outline, with the base of the mushroom oriented adaxially (Fig. 12a). This is typical of dryopteroid ferns (Moran, 1986, 1987; pers. obs.). Aerophores run down the sides of the petiole and are evident in cross section by a gap in the thickened peripheral collenchyma of the petiole. The petiole bases do not persist or accumulate starch after the rest of the leaf has withered. In other words, *Stigmatopteris* lacks trophopods.

Spores. I examined the spores from 11 species of *Stigmatopteris* with the scanning electron microscope (SEM). All of the spores were typical of those found elsewhere in the Dryopteridaceae, being monolet, having a smooth exospore, and showing a broadly inflated or narrowly folded perispore (Fig. 5). The inner layer of the perispore is thin and usually adheres to the smooth exospore; the outer layer is thicker and compact.

The perispore surface on and between the folds was nearly uniform in all 11 species examined (Fig. 5). The surface is relatively unornamented, being either smooth (Fig. 5f) or beset with low, diffuse ridges (Fig. 5c, d). Because of the uniformity, the spores do not provide helpful characters in the subgeneric taxonomy of the genus.

Ornamentation of the perispore differs in *Stigmatopteris* from that of the most closely related

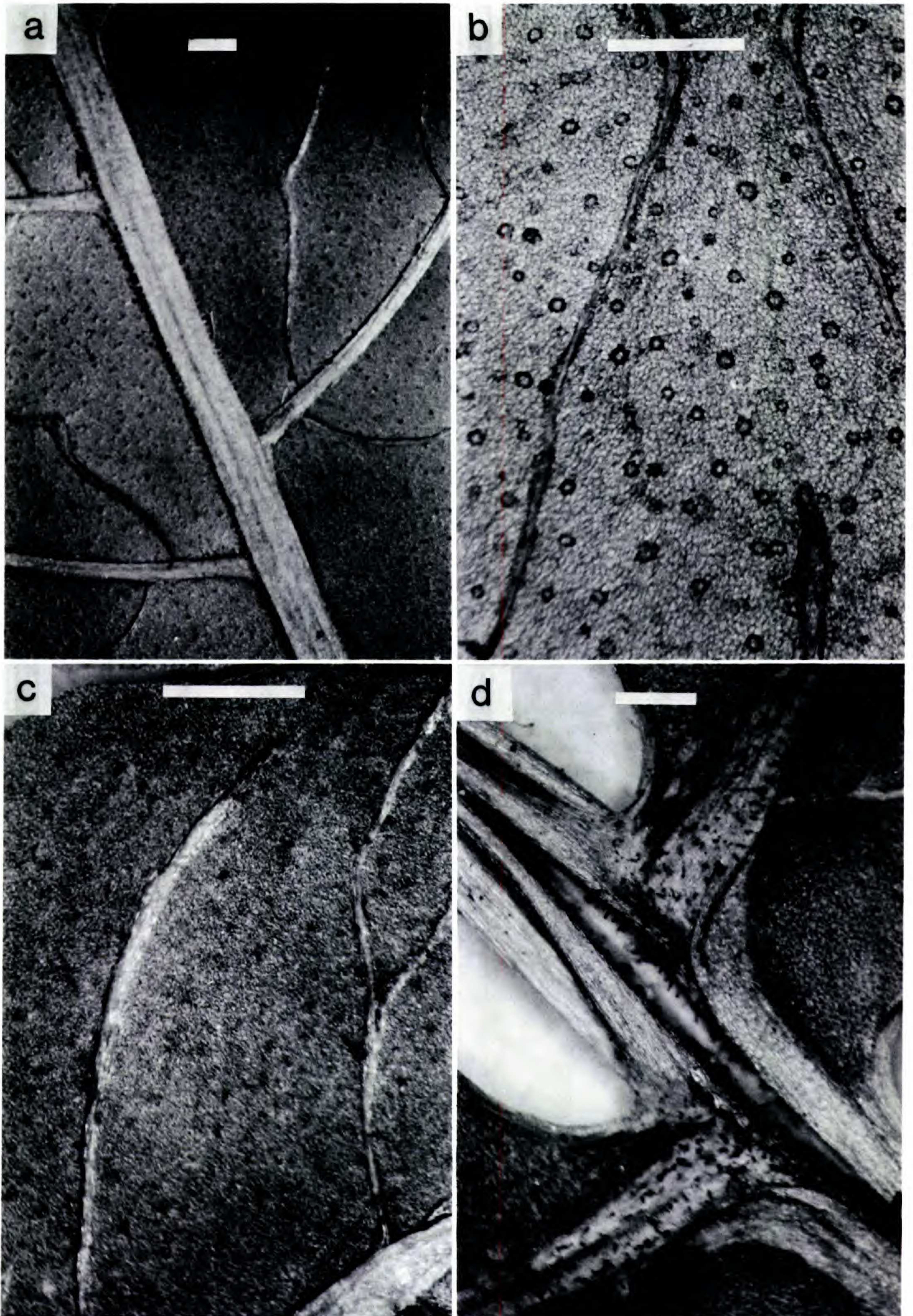


FIGURE 3. Internal punctate glands in the lamina of *Stigmatopteris* (a-c) and rachis-costa juncture showing adaxial grooves pubescent with short hairs (d). White bars indicate 1 mm.—a, b. *S. bulbifera* (Øllgaard et al. 35866, AAU).—c. *S. contracta* (Moran 3330, MO).—d. *S. heterocarpa* (Haerchen 106, B).

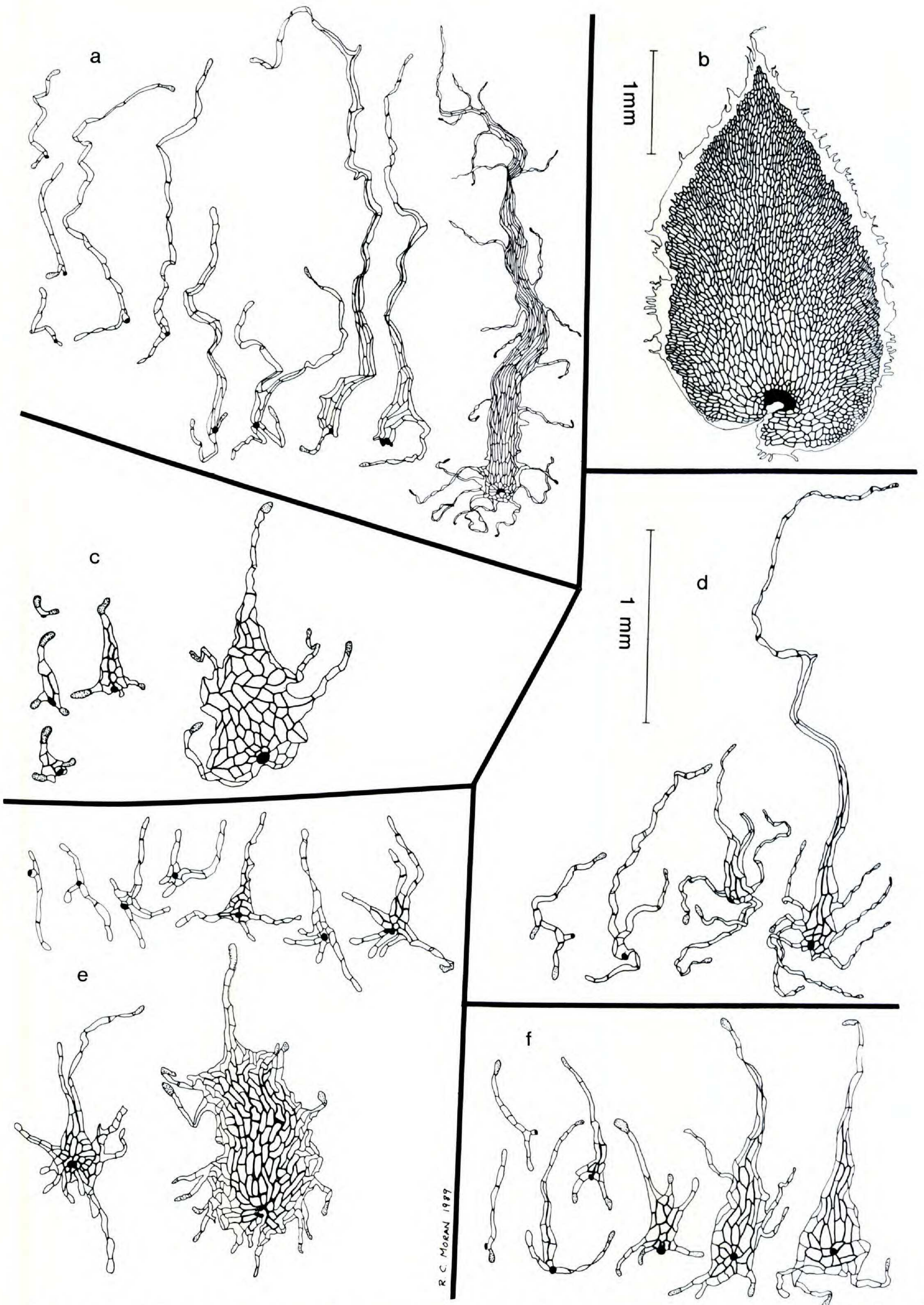
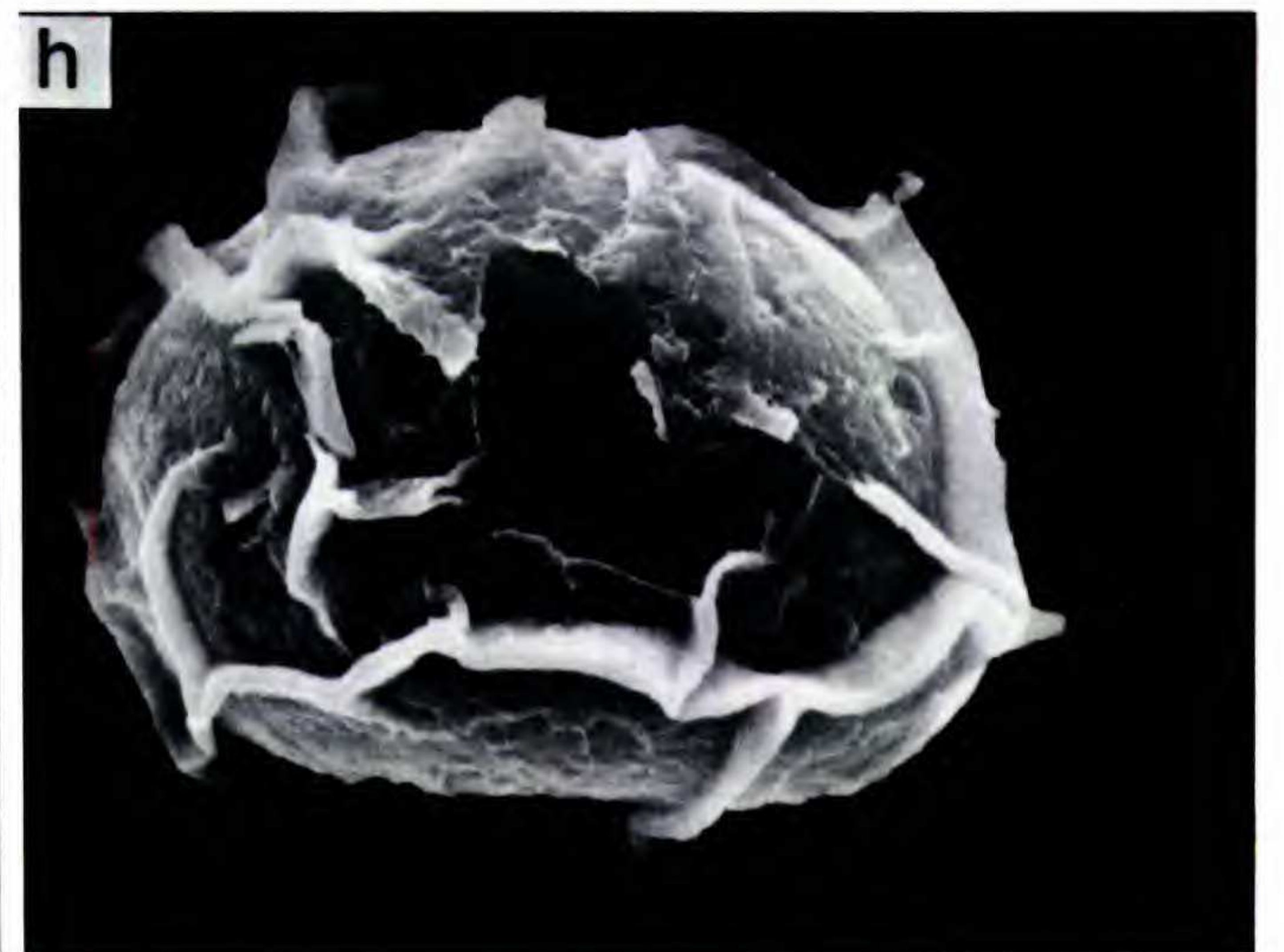
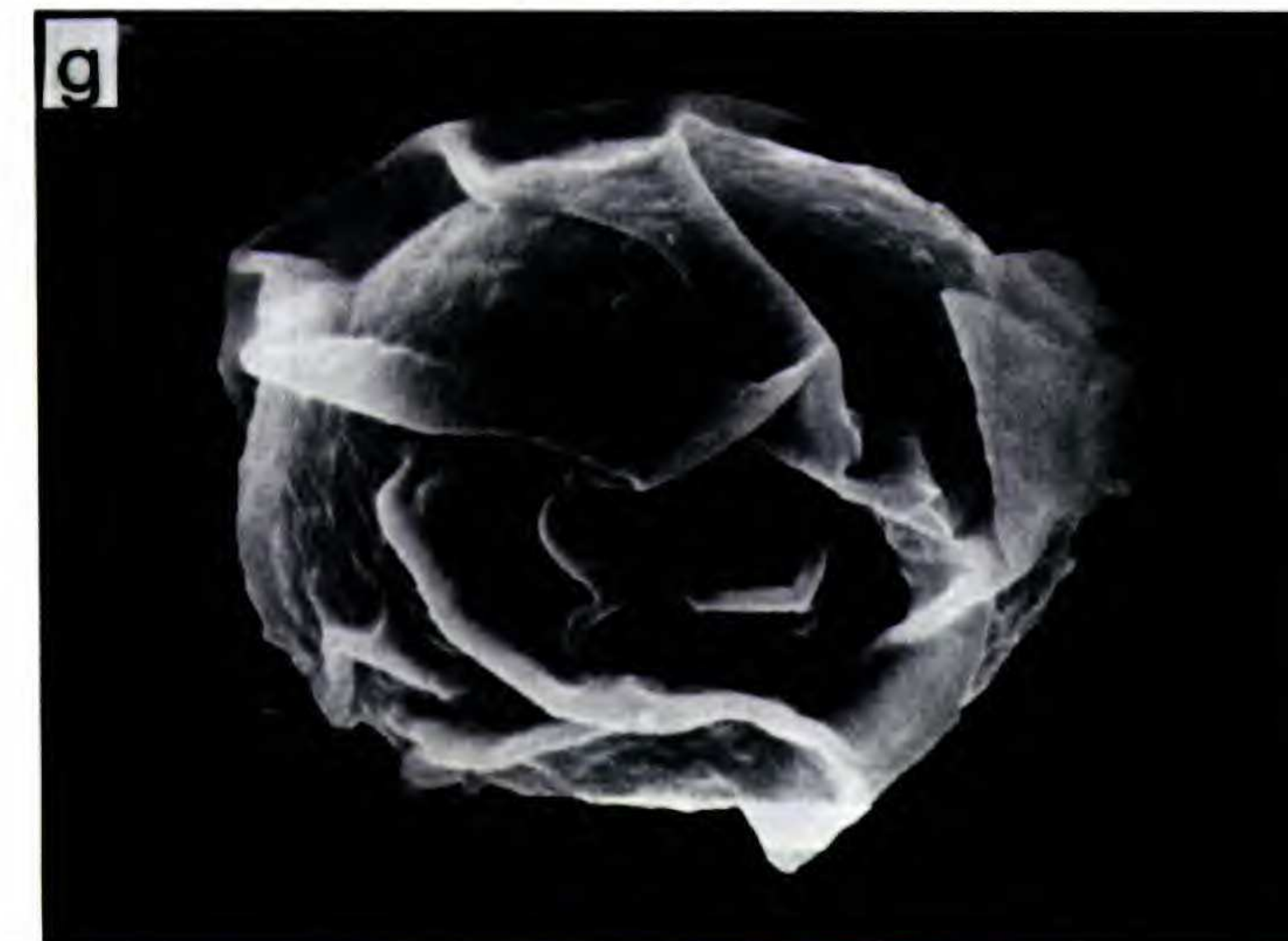
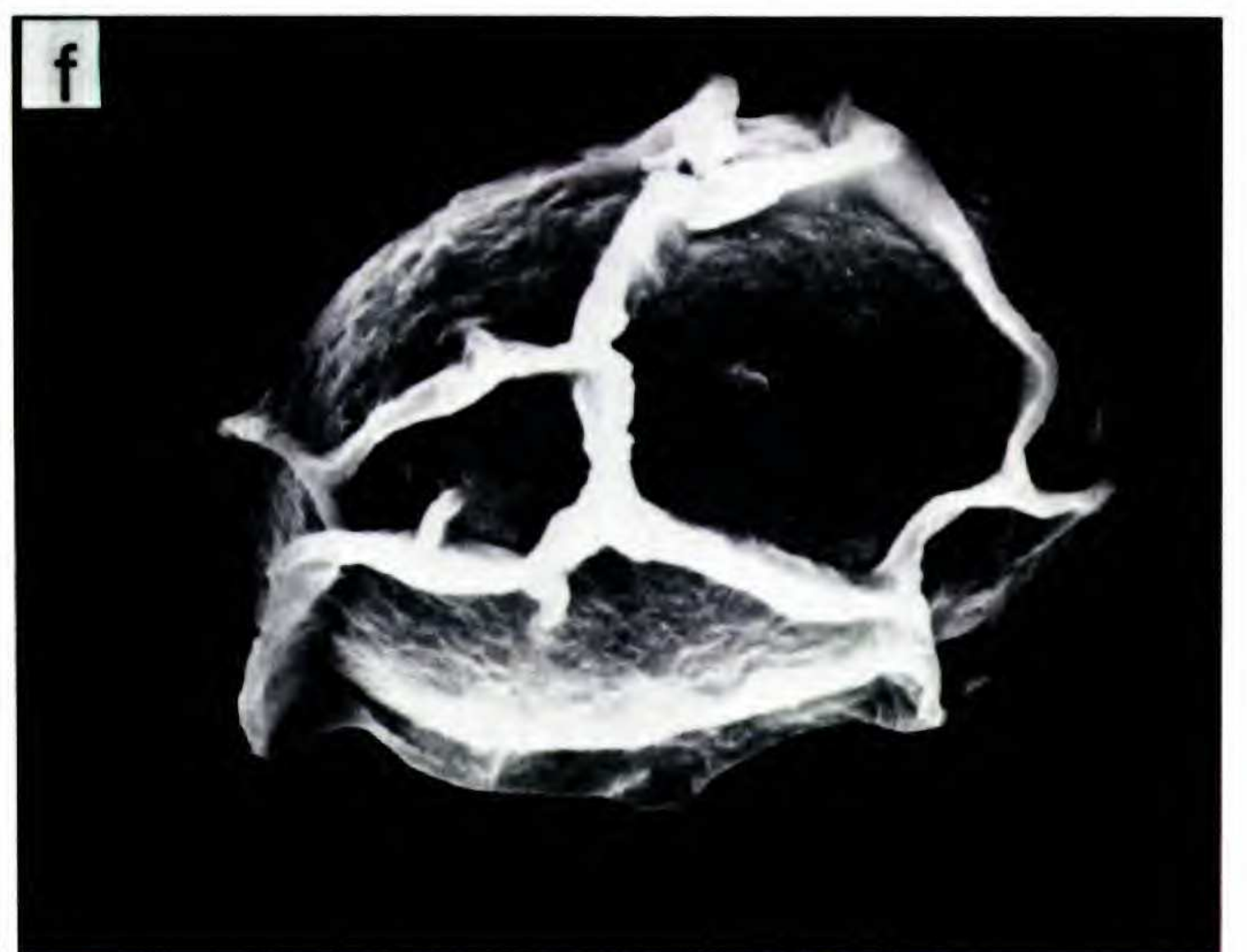
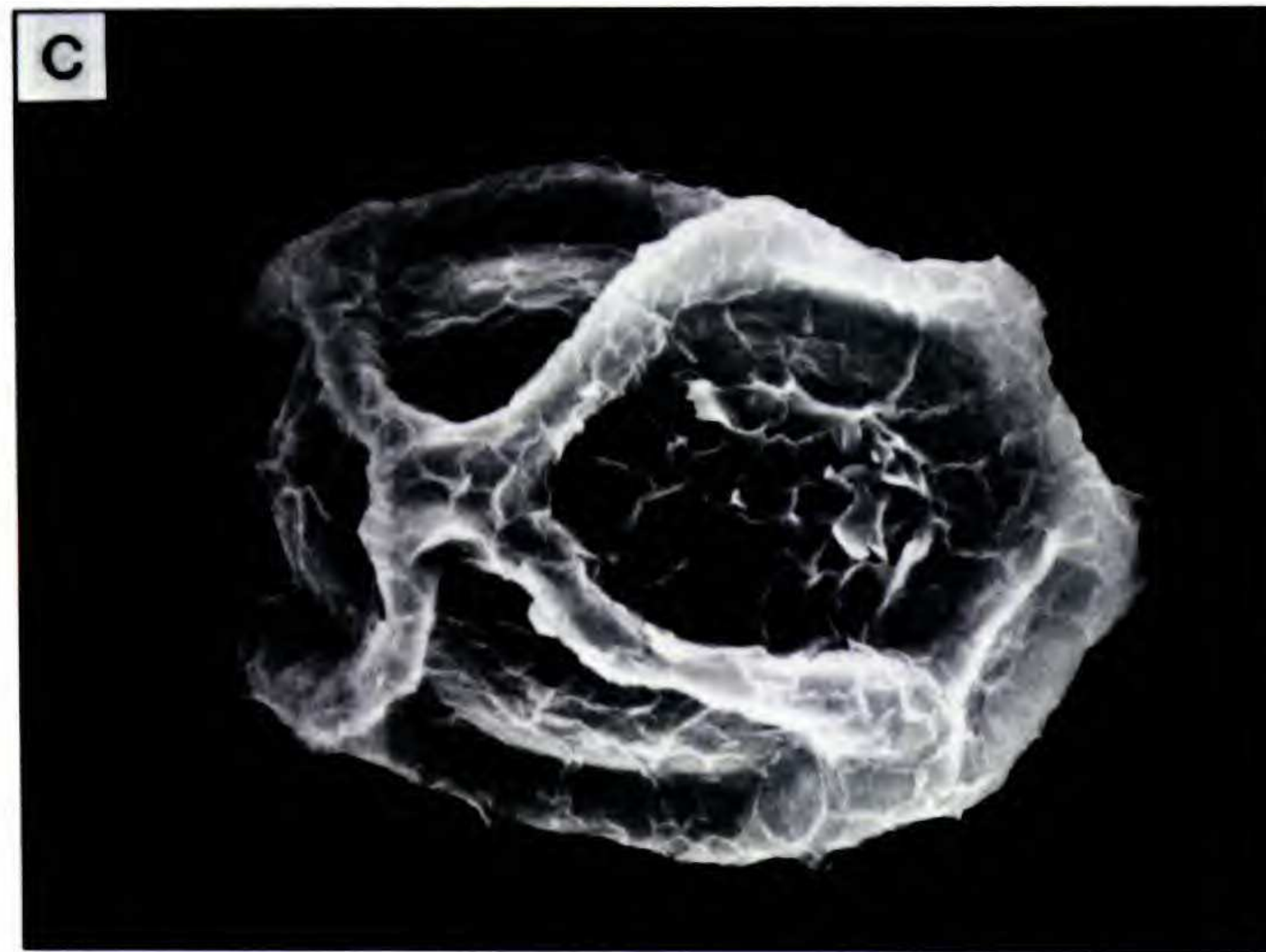
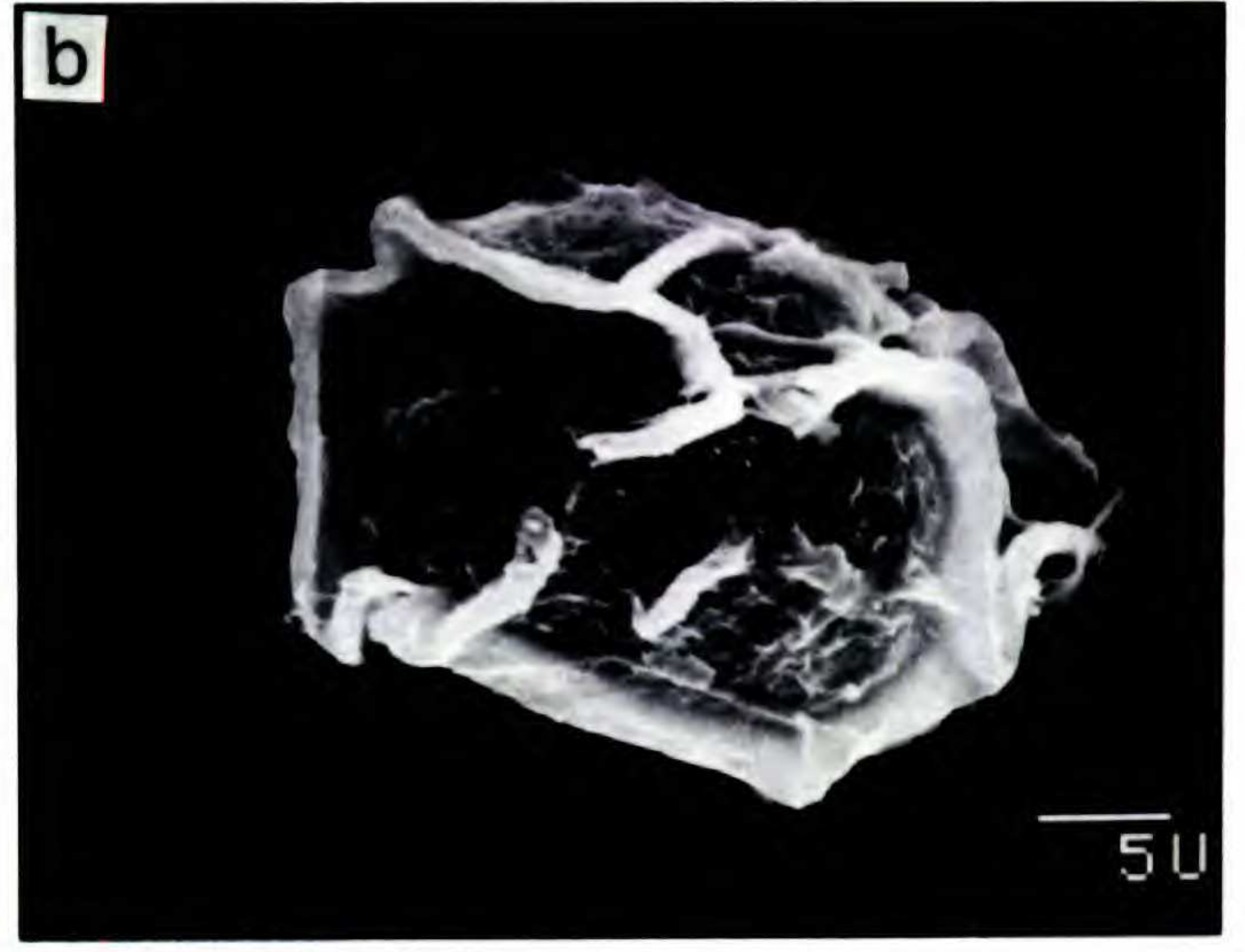
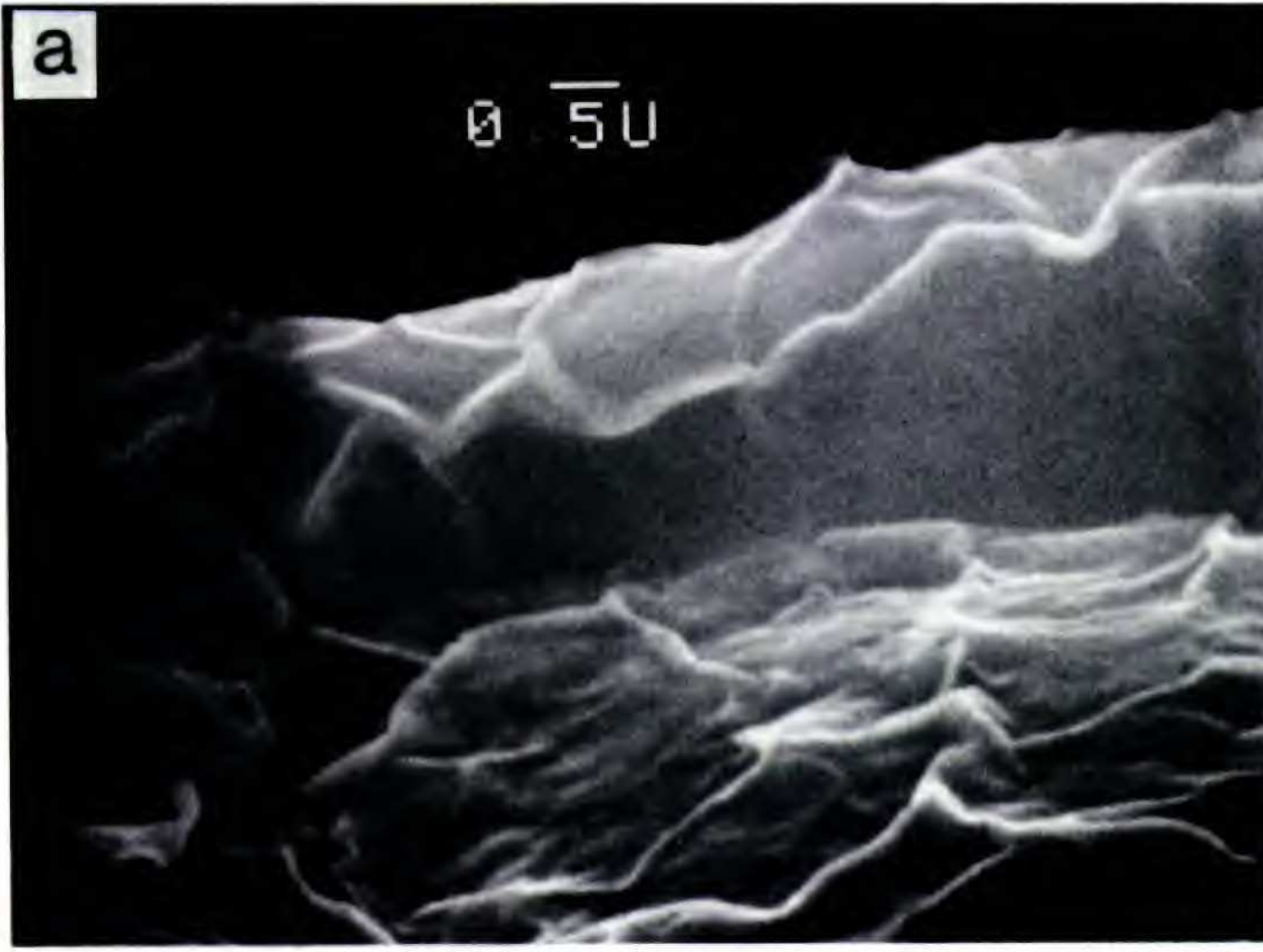


FIGURE 4. Scales of *Stigmatopteris*. The scale shown in b is from a petiole base; all others are from the abaxial surface of the lamina and show the transition from uniseriate scales (proscapes or microscales) to multiseriate ones. All are the same magnification as shown in d, except b and the far right scale in a.—a. *S. pellucidopunctata* (Moran 3624, MO).—b. *S. ichthiosma* (Moran 3545, MO).—c. *S. sordida* (Gómez 18641, CR).—d. *S. lechleri* (Moran 3582, MO).—e. *S. opaca* (Moran 3576, MO).—f. *S. sordida* (Moran 3315, MO).



dryopteroid genera, i.e., *Polybotrya*, *Cyclodium*, and *Olfersia*. These genera have more ornamentation on the perispore. For example, the spores of *Polybotrya* are typically densely echinate (Moran, 1987; Tryon & Tryon, 1982); those of *Cyclodium* are usually finely papillate but can be variously ornamented (Smith, 1986; Tryon & Tryon, 1982); and those of *Olfersia* are sparsely echinate (Moran, 1986; Tryon & Tryon, 1982).

Although these types of spore ornamentation are distinct, it is premature to determine which type is ancestral and which is derived. Such a determination must await a comprehensive comparative study of perispore ornamentation in the Dryopteridaceae. Therefore, I have not used spore ornamentation in the cladogram for *Stigmatopteris* and related genera (Fig. 6).

CHROMOSOME NUMBER

Walker (1966), who has made the only chromosome count for *Stigmatopteris*, found that $n = 41$ in *S. jamaicensis* (reported as *S. nothochlaena*, a synonym). This number relates the genus to the dryopteroid ferns.

Walker also noted that meiosis occurs very early in *Stigmatopteris* during the crozier stage of leaf development. Unfortunately, most workers (including myself) have collected samples for chromosome counts past the crozier stage, at a stage more typical for ferns in general, i.e., when the sori are small and white, but on expanded leaves beyond the crozier stage. This probably explains why only one count exists for the genus.

EVOLUTIONARY RELATIONSHIPS

Family relationships. That *Stigmatopteris* is a member of the Dryopteridaceae (sensu stricto of Holttum, 1984) is clearly shown by several characteristics which it shares with all genera of that family: $x = 41$, more than three vascular bundles in the petiole and these arranged in an omega shape when viewed in cross section (Fig. 12a), and grooves on the adaxial surface of the axes that are decurrent into those of the next lower order. The Dryopteridaceae are closely related to the Tectariaceae (sensu stricto of Holttum, 1984), but *Stigmatopteris* differs from the latter family by lacking *Cteni-*

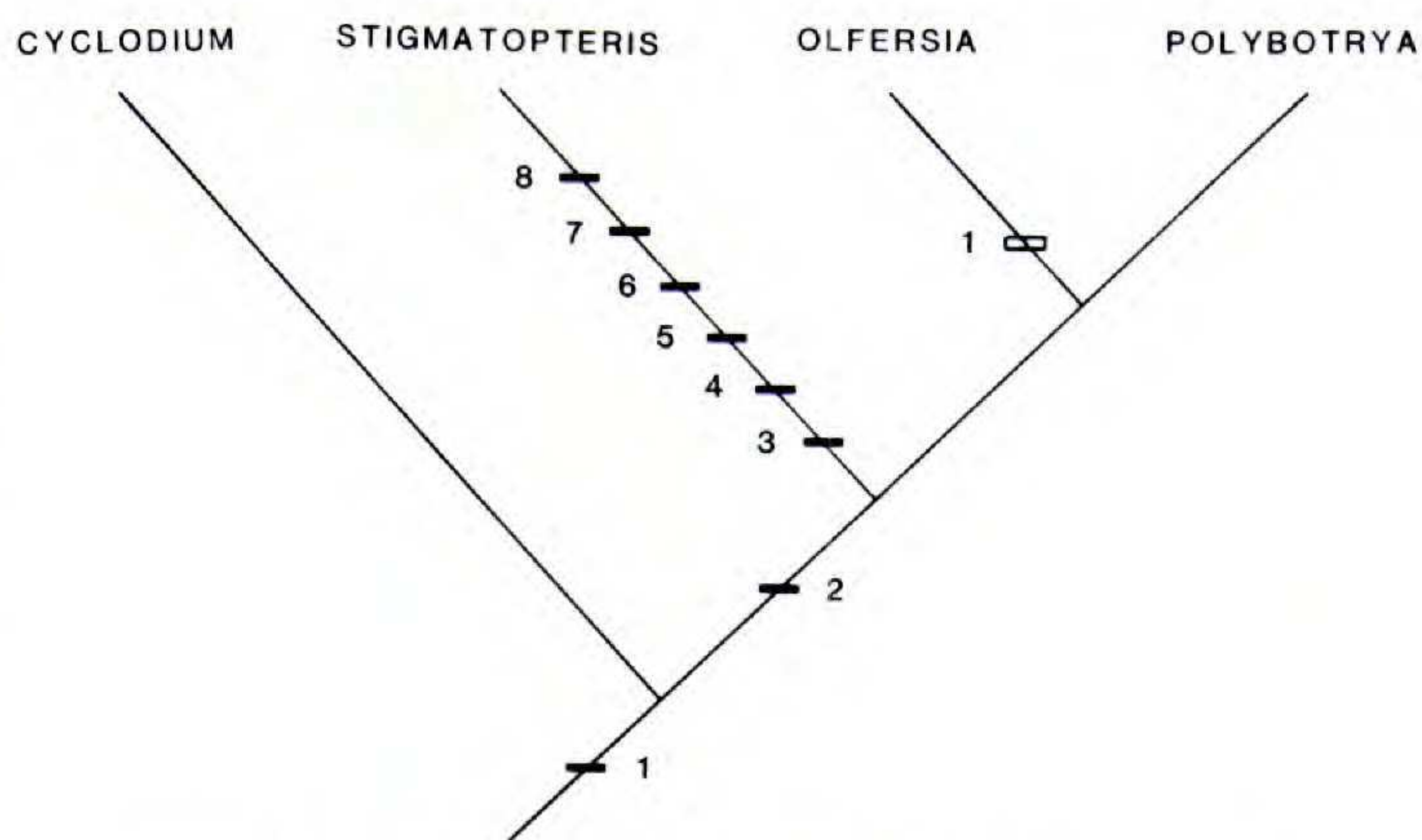


FIGURE 6. Cladogram of *Cyclodium*, *Stigmatopteris*, *Olfersia*, and *Polybotrya*. The numbered black bars represent the derived character states given in Table 4. The open bar below *Olfersia* represents a character state reversal. See Moran (1986) for the additional apomorphies and synapomorphies pertaining to *Olfersia* and *Polybotrya*.

tis hairs (i.e., small catenate, several-celled hairs with the color aggregated in the cross walls), and having sulcate, decurrent axial grooves.

Generic relationships. *Stigmatopteris* most closely resembles *Cyclodium* (sensu Smith, 1986), another dryopteroid genus, as shown by similarities in leaf cutting and venation and by the laminae, which are hairless except for the grooves of the rachis and costae. In fact, the two genera are so similar in these respects that some pteridologists (e.g., Christensen, 1913, 1920; Tryon & Tryon, 1982) have regarded them as one. They are, however, best kept as distinct. The two genera exhibit 11 morphological differences (Table 3), and this is more than that which occurs between other pairs of dryopteroid genera, such as *Arachniodes* and *Dryopteris*, *Arachniodes* and *Maxonia*, or *Cyrtomium* and *Polystichum*. If there is to be consistency in recognizing dryopteroid genera, at least as regards the number of characters that separate them, then *Cyclodium* and *Stigmatopteris* should be maintained as distinct.

In the Dryopteridaceae, *Stigmatopteris* and *Cyclodium* form a clade with *Polybotrya* and *Olfersia* (Fig. 6, Table 4). This clade is defined by the presence of hairs in the adaxial grooves of the axes (Fig. 3d). This character state is considered synapomorphic because all other dryopteroid ferns (sensu stricto) are hairless in the adaxial grooves of the axes. This character state would be weak if

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FIGURE 5. Spores of *Stigmatopteris*. —a, c. *S. longicaudata* (Mickel 6392, NY). —b. *S. lechleri* (von Sneidern 5046, US). —d. *S. tyucana* (Brade 5892, NY). —e. *S. opaca* (Øllgaard et al. 35859, AAU). —f. *S. sordida* (Moran 3315, MO). —g. *S. rotundata* (Cremers 9140, UC). —h. *S. caudata* (Webb s.n., NY). Spores c–h the same scale as in b.

TABLE 3. Comparison of *Stigmatopteris* and *Cyclodium*.

SIMILARITIES		
Hairs of the lamina: lacking (except in grooves of the rachis and costae).		
Hairs in grooves of the rachis and costae: 0.05–0.2 mm long, usually blunt-tipped, colorless, one- to few-celled.		
Lamina cutting: similar in many species, cf. <i>S. rotundata</i> and <i>C. guianense</i> , or <i>S. opaca</i> and <i>C. meniscioides</i> .		
Venation: similar in free-veined species such as <i>S. nephrodioides</i> and <i>C. guianense</i> , and in anastomosing-veined species such as <i>S. heterophlebia</i> and <i>C. meniscioides</i> .		
DIFFERENCES		
Character	<i>Stigmatopteris</i>	<i>Cyclodium</i>
Indusium:	absent	present
Lamina texture:	papyraceous	chartaceous or coriaceous
Pinnule arrangement:	anadromous basally, catadromous distally	anadromous throughout
Position of vein ending:	behind margin	at margin
Shape of vein tips:	clavate	slender
Internal laminar glands:	present	absent
Scale frequency on axes:	common	rare or lacking
Scale color:	light brown or orangish	dark brown
Scale texture:	thin	thick
Marginal teeth of scales:	uniseriate	composed of upturned margins from two adjacent cell walls
Gland at the apex of scale teeth:	present	absent
Geography:	primarily Andean	primarily Guianan

nothing else correlated with it; it could have evolved more than once, and if so the clade would be polyphyletic. The hypothesis that this character evolved only once is supported by the fact that the type of pubescence is the same in all the genera: the hairs are 0.05–0.2 mm long, usually blunt-tipped, colorless, and one- to few-celled (Smith, 1986; Moran, 1987, fig. 10b–e, g, h). *Olfersia cervina*, the only species of *Olfersia*, is an exception, having glabrous grooves. Because *Olfersia* is the sister genus to *Polybotrya* (Moran, 1986), its lack of hairs in the grooves is best interpreted as a character state reversal (Fig. 6). Some species

of *Polybotrya* subg. *Polybotrya*, such as *P. osmundacea* and *P. cyatheoides*, have much longer hairs in the grooves (Moran, 1987, fig. 49c) than those found in the grooves of *Cyclodium* and *Stigmatopteris*. These longer hairs, however, are otherwise similar to the smaller ones and are probably derived from them.

The clade with *Stigmatopteris*, *Olfersia*, and *Polybotrya* is defined only by one synapomorphy: loss of the indusium (Fig. 6, Table 4). This synapomorphy is weak and therefore considered tentative because no others correlate with it. Furthermore, the number of times the indusium has been lost in

TABLE 4. Characters and character states used in the cladistic analysis of *Stigmatopteris*, *Cyclodium*, *Olfersia*, and *Polybotrya* (Fig. 6). Character state polarities were determined by comparison to other genera in the Dryopteridaceae, such as *Arachniodes*, *Dryopteris*, and *Polystichum*.

Character	Ancestral condition	Derived condition
1. Pubescence in adaxial grooves of the axes	absent	present
2. Indusium	present	absent
3. Large glands in the lamina	absent	present
4. Marginal teeth or processes of the scales	composed of the upturned margins from two adjacent cells	uniseriate
5. Glandular cell at apex of scale teeth or processes	absent	present
6. Vein termination	at margin	behind margin
7. Shape of vein tip	slender	clavate
8. Texture of lamina	papyraceous or chartaceous	membranaceous

TABLE 5. Data matrix used in the cladistic analysis of 23 species of *Stigmatopteris*, with *Cyclodium* used as the outgroup. See Table 6 for the meaning of characters and character states.

Taxon	Characters								
	1	2	3	4	5	6	7	8	9
<i>Cyclodium</i>	0	0	0	0	0	0	0	0	0
<i>S. pterorhachis</i>	0	0	1	1	4	0	0	0	1
<i>S. bulbifera</i>	0	1	1	1	4	0	1	0	1
<i>S. heterophlebia</i>	0	0	1	1	4	0	1	0	1
<i>S. killipiana</i>	0	0	1	0	4	0	0	0	1
<i>S. opaca</i>	0	0	1	0	4	0	0	0	1
<i>S. longicaudata</i>	0	0	0	1	4	0	0	0	0
<i>S. heterocarpa</i>	0	0	0	0	4	0	0	0	0
<i>S. rotundata</i>	0	0	0	0	3	0	0	0	0
<i>S. prionites</i>	0	0	0	0	3	0	0	0	0
<i>S. nephrodioides</i>	0	0	0	0	3	0	0	0	0
<i>S. michaelis</i>	0	0	0	1	2	0	0	0	0
<i>S. tyucana</i>	0	0	0	0	3	0	0	0	0
<i>S. chimalapensis</i>	0	0	0	0	3	0	0	0	0
<i>S. jamaicensis</i>	1	0	0	0	1	0	0	0	0
<i>S. hemiptera</i>	0	1	0	0	2	1	0	0	0
<i>S. gemipara</i>	0	1	0	0	2	0	0	0	0
<i>S. brevinervis</i>	0	0	0	0	2	0	0	0	0
<i>S. contracta</i>	1	0	0	0	1	0	0	1	0
<i>S. caudata</i>	0	0	0	0	1	1	0	0	0
<i>S. ichthiosma</i>	1	0	0	0	1	0	0	1	0
<i>S. sordida</i>	0	0	0	0	2	0	0	1	0
<i>S. pellucidopunctata</i>	0	0	0	0	2	0	0	1	0
<i>S. lechleri</i>	0	0	0	0	0	0	0	0	0

fern evolution suggests that it could have easily been lost independently in *Stigmatopteris* and in the *Olfersia-Polybotrya* clade.

Species relationships. A cladogram of species relationships was constructed using the HENNIG86 program, version 1.5 (Farris, 1988; Platnick, 1989), run on a Dell System 200 computer applying the implicit enumeration option for calculating trees. Table 5 shows the data matrix used in the analysis, and Table 6 lists the characters and character states used in the data matrix. *Stigmatopteris ulei* was not included in the data matrix because it appears to be of hybrid origin. Another feature of HENNIG86 was also used: the successive weighting procedure, which calculates weights from the best fits to the most parsimonious trees using rescaled consistencies (rc), which are the products of the character consistency (c) and the character retention index (r). The product is scaled to lie in the range 0–10 (Table 7). The weighting procedure is repeated on successively produced trees until the trees no longer change (Farris, 1988).

Cyclodium was used as the outgroup to determine character state polarities in Table 6 (see section on generic relationships for justification of using *Cyclodium* as the outgroup). All species of

Cyclodium have the ancestral character states given in Table 4 for characters 1, 2, 4, 6, 7, and 8; therefore, it was simple to determine polarity. However, because *Cyclodium* has both character states for characters 3, 5, and 9 (Table 6), it could not be used to determine character state polarity. For

TABLE 6. Characters and character states used in the cladistic analysis of 23 species of *Stigmatopteris* (the probable hybrid *S. ulei* not included). The ancestral state equals 0; the derived state (s) equals 1 (or more). The hypothesized evolutionary pathways for all the character states are unilinear.

1. Indusial scale: absent (0); present (1).
2. Buds: absent (0); 1 = present (1).
3. Veins: free (0); anastomosing (1).
4. Distal pinnae bases: short-decurrent (0); long-decurrent (1).
5. Lamina dissection: 2-pinnate-pinnatifid (0); nearly 2-pinnate (1); pinnae cut 1/2–3/4 to the costa (2); pinnae cut 1/2–3/4 to the costa (3); entire or nearly so (4).
6. Basal basiscopic lobe of the distal pinnae: adnate to costa (0); adnate to the rachis (1).
7. Hairs on rachis and costa: absent (0); present (1).
8. Petiole scale texture: thin, flaccid (0); thick, rigid (1).
9. Number of pinna pairs: 12–18 (0); 1–12 (1).

TABLE 7. Character consistencies (c) and retention indices (r) as the best fits on the three equally parsimonious trees from HENNIG86, which was used to calculate weights. Final weights were often the third round of successive weighting procedures in HENNIG86. Weights were truncated to integers.

Char-acter	Range of steps	Num-ber of steps	Con-sist-ency index (c)	Reten-tion index (r)	Weight (rc × 10)	Final weight
1	1	1	1	1	10	10
2	1	2	0.5	0.5	2	2
3	1	1	1	1	10	10
4	1	3	0.3	0.5	1	1
5	4	4	1	1	10	10
6	1	2	0.5	0	0	0
7	1	1	1	1	10	10
8	1	2	0.5	0.7	3	3
9	1	1	1	1	10	10

these three characters, polarity was determined by deferring to Holttum's (1968) hypotheses about the general trends in fern evolution. This method is not entirely satisfactory, but in this case it is the best that could be done with present knowledge.

Regarding character 3 (free vs. anastomosing veins), Holttum (1968) believed that the evolutionary trend has been from free to anastomosing. Therefore, free veins were assigned as the ancestral character state (Table 6). He also believed that the earliest ferns had highly divided leaves and that the evolutionary trend has been toward less divided leaves. Accordingly, character 5 (leaf division) has the most divided leaf as the ancestral state and the least divided leaf (1-pinnate with entire pinnae) the derived state. Finally, for character 9, Holttum believed that the evolutionary trend has been to develop fewer pinnae; therefore, the smaller number of pinnae was considered as the derived state.

HENNIG86 found three equally most-parsimonious cladograms (Fig. 7), which differed only in the branching patterns for seven of the most derived species—a group that consists primarily of species with anastomosing veins and entire to shallowly lobed pinnae. All of the trees had 17 steps and a consistency index of 0.7. Cladogram 2 (Fig. 7) has two character state sequences. The one shown involves a reversal of character 4 at the node that defines *S. opaca* and *S. killipiana*. The other sequence assumes a parallelism of character state 4.1 at the line leading to *S. longicaudata* and at the node which defines *S. pterorhachis*, *S. bulbifera*, and *S. heterophlebia*. I do not

believe that one of these sequences is more likely than the other; both seem equally probable.

At the beginning of this study, I thought that species from different regions might form monophyletic groups, such as the six species from southeastern Brazil, or the three species from the Greater Antilles, or the eleven species from the Andes. Although two of the species endemic to the Greater Antilles proved to be sister species, no general correlation exists between the cladogram and the geography of the other species. In other words, no synapomorphy exists that holds together the species from these regions.

The species with anastomosing veins and entire to shallowly lobed pinnae are distinctive and form a monophyletic group (Fig. 7, trees 1, 2, 3). They could be considered a subgenus, much the same way that *Soromanes* is considered a subgenus of *Polybotrya* (Moran, 1987). However, *S. longicaudata* is intermediate between the group and the rest of the genus, and so I have not formally named the group.

Key and Descriptions

Stigmatopteris C. Chr., Bot. Tidsskr. 29: 292. 1909. TYPE: *Stigmatopteris rotundata* (Willd.) C. Chr.

Dryopteris subg. *Stigmatopteris* (C. Chr.) C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. ser. 7, 10: 73. 1913.

Plants terrestrial; rhizome short-creeping, scaly at the apex, the meristemes surrounded by whitish parenchyma (not darkened sclerenchymatous sheaths); petioles with 4 to many vascular bundles in cross section (Fig. 12a), continuous (not articulate) with the rhizome; lamina 1-pinnate to 2-pinnate-pinnatifid, the apex pinnatifid, the tissue glabrous on both surfaces, with punctate glands in the mesophyll (Fig. 3a-c); pinnae linear to narrowly oblong, often with a decurrent basal wing, the apices attenuate and serrate; pinnae or segments arranged anadromically in the proximal pinna pairs, becoming catadromically arranged in the distal pinna pairs; adaxial surface of the rachis and costae sulcate, the sulci decurrent into those of the next lower order, pubescent adaxially within the grooves (Fig. 3d), the hairs 0.05–0.2 mm, 1- or 2-celled, colorless, usually blunt-tipped; abaxial surface of the rachis and costae stramineous or occasionally brown, lacking hairs abaxially or (in two species) glandular-pubescent, scaly, the scales thin, translucent, light brown to orangish, ciliate or denticulate, the cilia or teeth terminating in a

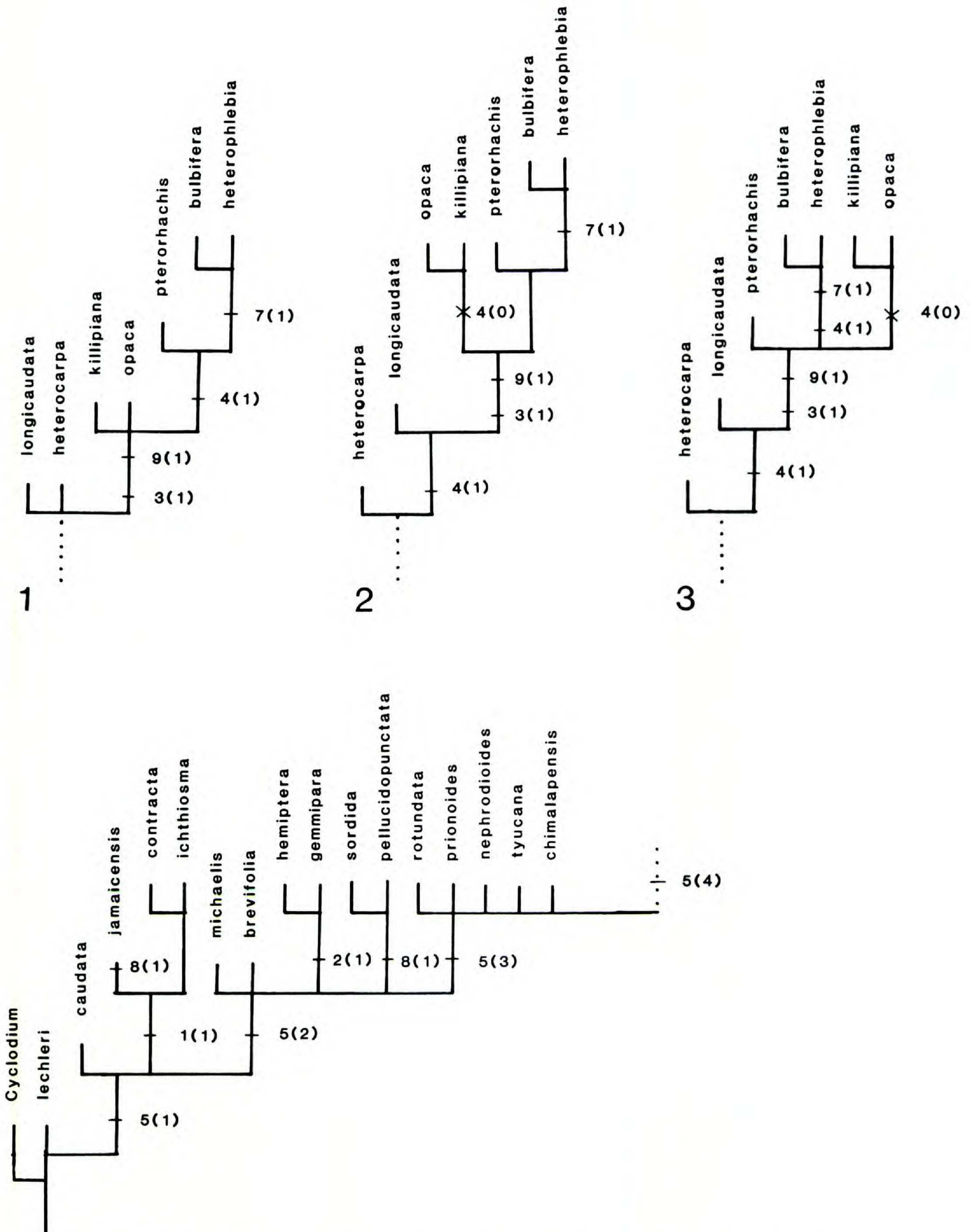


FIGURE 7. Cladogram of species relationships in *Stigmatopteris*. Cladograms 1, 2, and 3 attach to dotted far right of the bottom tree. Cross bars indicate apomorphies; the × in cladograms 2 and 3 indicate reversals.

darkened, slightly enlarged, glandular cell (Fig. 4); veins either free or inconsistently anastomosing (i.e., mostly anastomosing but with a readily noticeable number of free veins), the tips clavate adaxially (hydathodous?), terminating before the

margin; sori round or slightly oblong near the costae; indusia absent; sporangial stalks not paraphysate; spores monolete, with broadly folded perispore and low, broken ridges (Fig. 5). Chromosome number, $x = 41$.

KEY TO THE SPECIES OF *STIGMATOPTERIS*

1a. Key to the species of the Antilles and southeastern Brazil.

2a. Species of the Antilles.

3a. Pinnae crenate or cut less than $\frac{1}{3}$ to the costa; Lesser Antilles 21. *S. rotundata* (Willd.) C. Chr.3b. Pinnae cut $\frac{1}{2}$ – $\frac{7}{8}$ to the costa; Greater Antilles.4a. Pinnae with the basal basispic lobe arising from the rachis (Fig. 14a); Cuba
..... 7. *S. hemiptera* (Maxon) C. Chr.

4b. Pinnae with the basal basispic lobe arising from the costa; Jamaica, Haiti.

5a. Lamina lacking buds; pinnae 15–23 cm, pairs 22–26; veins 8–11 per segment; sori
covered by an indusiumlike scale; petiole ca. half the length of the lamina; Jamaica
..... 11. *S. jamaicensis* (Desv.) Proctor5b. Lamina bearing buds; pinnae (4–)9–14 cm, pairs 9–20; veins 5–7(–8) per segment; sori
lacking an indusiumlike scale; petiole equaling the length of the lamina; Jamaica, Haiti
..... 6. *S. gemmipara* C. Chr.

2b. Species of southeastern Brazil.

6a. Pinnae cut $\frac{1}{2}$ or less to the costa; veins 3–7 per lobe.7a. Pinnae entire to lobed less than $\frac{1}{4}$ to the costa 8. *S. heterocarpa* (Fée) Rosenstock7b. Pinnae lobed $\frac{1}{3}$ – $\frac{1}{2}$ to the costa.8a. Sori inframedial; fertile pinnae 1.1–2.3 cm wide, the sinuses broad, U-shaped
..... 19. *S. prionites* (Kunze) C. Chr.8b. Sori medial to suprasedial; fertile pinnae 2.5–4 cm wide, the sinuses narrow, V-shaped
..... 23. *S. tyucana* (Raddi) C. Chr.6b. Pinnae cut $\frac{1}{2}$ – $\frac{7}{8}$ to the costa; veins 5–15 per lobe.9a. Pinnae cut $\frac{2}{3}$ – $\frac{7}{8}$ to the costa, the distal ones often with the basal basispic lobe adnate and
ca. perpendicular to the rachis; (Fig. 10b); veins 9–15 per lobe .. 3. *S. caudata* (Raddi) C. Chr.9b. Pinnae cut $\frac{1}{2}$ – $\frac{2}{3}$ to the costa, the distal ones lacking a basal basispic lobe adnate to the
rachis; veins 5–8(–10) per lobe.10a. Sinuses narrow, V-shaped 1. *S. brevinervis* (Fée) R. C. Moran10b. Sinuses broad, U-shaped 24. *S. ulei* (Christ) Sehnem

1b. Key to all species (including those of the Antilles and southeastern Brazil).

11a. Veins anastomosing.

12a. Rachis and costae puberulent abaxially.

13a. Free pinna pairs 7–10; buds often present in the axils of the medial and distal pinnae
(these best seen adaxially) 2. *S. bulbifera* R. C. Moran13b. Free pinna pairs 1–3(–4); buds absent or (in Ecuador) rarely present
..... 9. *S. heterophlebia* (Baker) R. C. Moran

12b. Rachis and costae lacking hairs abaxially.

14a. Petiole abaxially atropurpureous, lustrous 12. *S. killipiana* Lellinger

14b. Petiole abaxially brown, tan, or stramineous, dull.

15a. Lamina thin, internal punctate glands easily visible (with magnification); sori round;
areoles of sterile leaves with 1 or 2 irregular, curved or forked excurrent veinlets;
western Venezuela, northern Colombia 20. *S. pterorhachis* R. C. Moran15b. Lamina thick, the internal punctate glands not visible (with magnification); sori
round or oblong with a strong tendency to become arcuate; areoles of sterile leaves
with 1 straight (or nearly so) excurrent veinlet (Fig. 24e); Ecuador, Peru
..... 17. *S. opaca* (Baker) C. Chr.

11b. Veins free or with a few casual anastomoses.

16a. Pinnae entire, crenate, or cut less than $\frac{1}{4}$ to the costa.17a. Pinnae confluent in the distal $\frac{1}{2}$ – $\frac{1}{3}$ of the lamina by a conspicuous, long-decurrent wing
(Fig. 21b) 14. *S. longicaudata* (Liebm.) C. Chr.17b. Pinnae confluent in the distal $\frac{1}{4}$ – $\frac{1}{8}$ of the lamina, the bases short-decurrent.18a. Pinna pairs 18–32; Lesser Antilles, Guianas, and eastern Venezuela
..... 21. *S. rotundata* (Willd.) C. Chr.18b. Pinna pairs 12–17; southeastern Brazil 8. *S. heterocarpa* (Fée) Rosenstock16b. Pinnae cut $\frac{1}{4}$ to all the way to the costa.19a. Pinnae confluent in the distal $\frac{1}{2}$ – $\frac{1}{3}$ of the lamina by a conspicuous, long-decurrent wing.20a. Pinnae (4.5–)9–11 cm; leaves 0.3–0.7 m; sori paraphysate with multicellular,
dark brown hairs 15. *S. michaelis* (Baker) C. Chr.20b. Pinnae 14–20 cm; leaves 0.8–1.4 m; sori not paraphysate or (in South America)
with filiform scales among the sporangia 14. *S. longicaudata* (Liebm.) C. Chr.19b. Pinnae confluent in the distal $\frac{1}{4}$ – $\frac{1}{8}$ of the lamina, the bases short-decurrent.21a. Distal pinnae with the basispic basal lobe adnate and ca. perpendicular to the
rachis (Figs. 10b, 14a), with the costule arising from the rachis.22a. Pinnae 4–7 cm wide; lamina lacking buds; veins 9–15 per segment; south-
eastern Brazil 3. *S. caudata* (Raddi) C. Chr.

22b. Pinnae 1.5–2.5 cm wide; lamina of small sterile leaves with buds in the axils

- of the distal pinnae; veins 6–10 per segment; Cuba
..... 7. *S. hemiptera* (Maxon) C. Chr.
- 21b. Distal pinnae with the basal basispic lobe adnate to the costa or only partly adnate to the rachis, the costule arising from the costa.
- 23a. Lamina 2-pinnate-pinnatifid 13. *S. lechleri* (Mett.) C. Chr.
- 23b. Lamina 1-pinnate-pinnatifid to nearly 2-pinnate.
- 24a. Costular scales bullate *or* buds present in the axils of the distal pinnae; Jamaica, Haiti.
- 25a. Pinnae 15–23 cm, pairs 22–26; lamina without buds in the axils of the distal pinnae; sori covered by an indusiumlike scale
..... 11. *S. jamaicensis* (Desv.) Proctor
- 25b. Pinnae (4–)9–14 cm, pairs 9–20; lamina with buds in the axils of the distal pinnae; sori not covered by an indusiumlike scale
..... 6. *S. gemmipara* C. Chr.
- 24a. Costular scales not bullate; buds absent in the axils of the distal pinnae; southern Mexico to southeastern Brazil.
- 26a. Bases of the medial pinnae overlapping the rachis (Figs. 12c, e, 23a); Costa Rica, Panama, northern Venezuela.
- 27a. Pinnae 3–6 cm wide, cut $\frac{3}{4}$ to nearly all the way to the costa; Costa Rica, Panama ... 5. *S. contracta* (Christ) C. Chr.
- 27b. Pinnae 2–3.5 cm wide, cut $\frac{1}{4}$ – $\frac{1}{2}$ to the costa; northern Venezuela 16. *S. nephrodioides* (Klotzsch) C. Chr.
- 26b. Bases of the medial pinnae not overlapping the rachis; southern Mexico to Bolivia, southeastern Brazil.
- 28a. Pinnae 8–12 cm; southern Mexico
..... 4. *S. chimalapensis* Mickel & Beitel
- 28b. Pinnae 12–40 cm.
- 29a. Pinnae 1.1–2.3 cm wide; veins 3–5 per lobe; southeastern Brazil. 19. *S. prionites* (Kunze) C. Chr.
- 29b. Pinnae 2–6 cm wide; veins 4–14 per lobe.
- 30a. Pinnae cut $\frac{1}{3}$ – $\frac{1}{2}$ to the costa; southeastern Brazil 23. *S. tyucana* (Raddi) C. Chr.
- 30b. Pinnae cut $\frac{1}{2}$ – $\frac{2}{3}$ to the costa.
- 31a. Sori subtended by an indusiumlike scale (Fig. 17b); western Ecuador
..... 10. *S. ichthiosma* (Sodiolo) C. Chr.
- 31b. Sori lacking an indusiumlike scale.
- 32a. Scales of the costae and costules lanceolate to linear, mixed with smaller fibrillose ones; Colombia to Bolivia
... 18. *S. pellucidopunctata* (C. Chr.)
C. Chr.
- 32b. Scales of the costae and costules ovate to lanceolate, filiform scales absent.
- 33a. Sori medial; southern Mexico to Ecuador
..... 22. *S. sordida* (Maxon)
C. Chr.
- 33b. Sori inframedial; southeastern Brazil.
- 34a. Sinuses narrow, V-shaped
... 1. *S. brevinervis* (Fée)
R. C. Moran
- 34b. Sinuses broad, U-shaped
..... 24. *S. ulei* (C. Chr.)
Sehnem

1. *Stigmatopteris brevinervis* (Fée) R. C. Moran, comb. nov. *Phegopteris brevinervis* Fée, Crypt. Vasc. Brésil 1: 243, t. 77, fig. 2. 1869. SYNTYPES: Brazil. Rio de Janeiro: Organ

Mountains, June 1869, *Glaziou* 3333 pro parte (lectotype, here designated, P); Organ Mountains, *Glaziou* 2400 pro parte (P). Figure 8. Map 1.

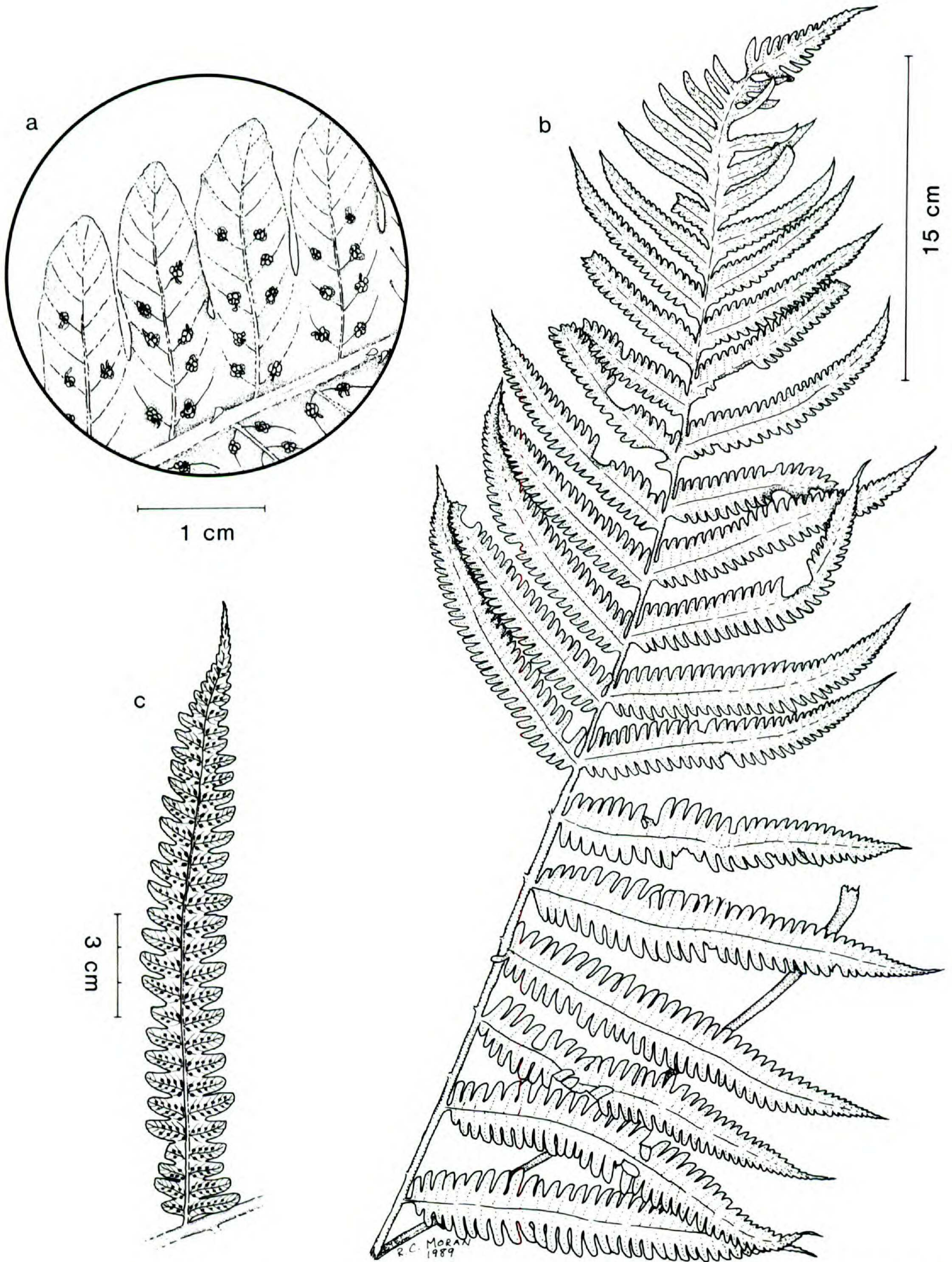
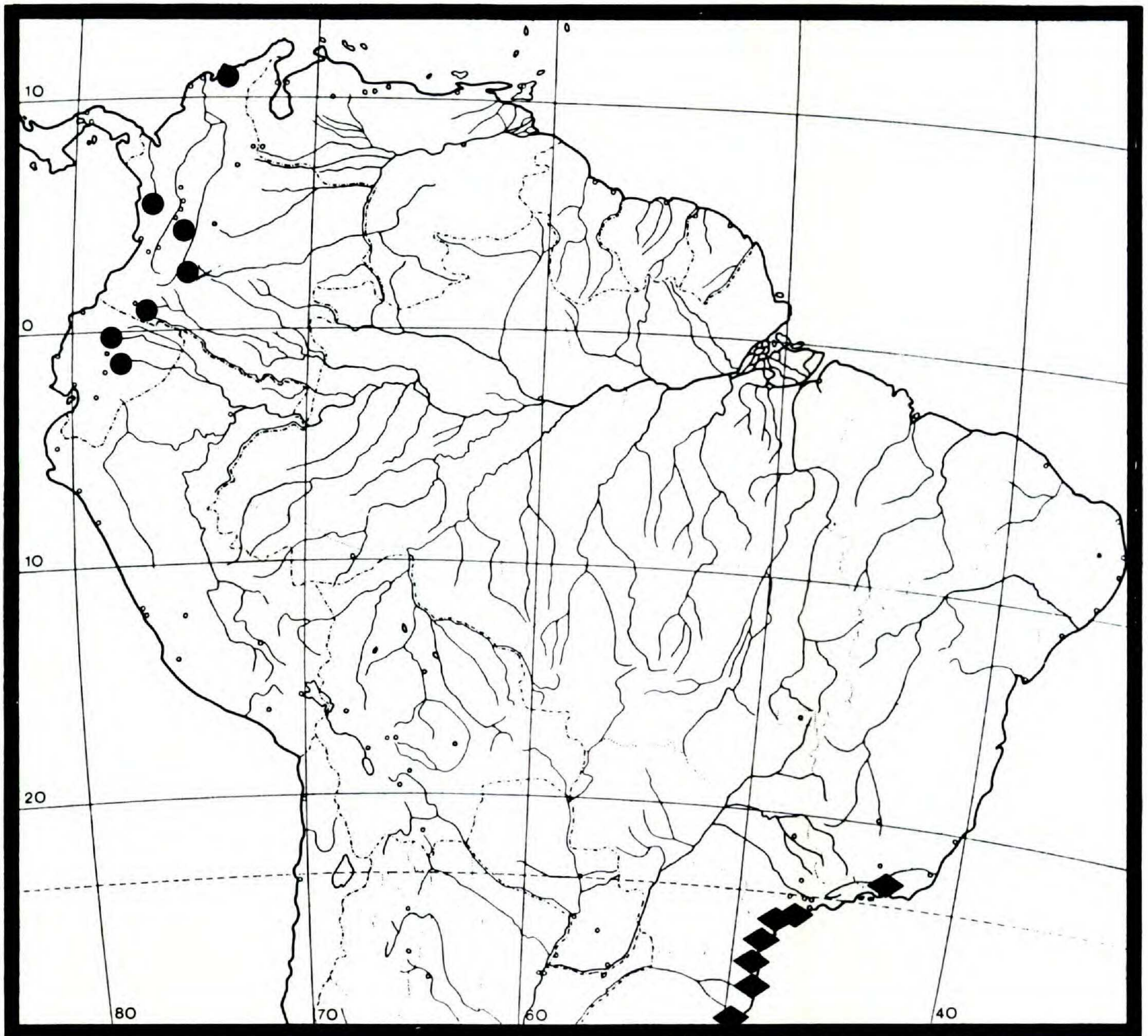


FIGURE 8. *Stigmatopteris brevinervis*.—a. Abaxial surface of a pinna (Brade 8250, UC).—b. Leaf (Dusén 725a, distal half, NY; proximal half, MO).—c. Fertile pinna (Glaziou 2400, P).



MAP 1. Distribution of *Stigmatopteris bulbifera* (dots) and *S. brevinervis* (diamonds).

Stigmatopteris bradei Rosenstock, Repert. Spec. Nov. Regni Veg. 21: 347. 1925. TYPE: Brazil. São Paulo: município Iguape, Serrinha, *Brade* 8250 (holotype, S? not seen; isotypes, PH, UC).

Rhizome short-creeping; leaves to 1.5 m; petiole ca. equaling the lamina, stramineous to brown, scaly at the base, the scales 5–12 × 1–2 mm, brown, thin, lanceolate; lamina 1-pinnate-pinnatifid, lanceolate, lacking bulblets, only a few distal-most pinnae with short-decurrent bases; pinnae 16–24 × 2.3–4 cm, 15–20 pairs, cut $\frac{1}{2}$ – $\frac{2}{3}$ to the costa, the base sessile or nearly so, the basal pinnae short-stalked; segments 5–6.5 mm wide, separated by narrow, V-shaped sinuses, entire to denticulate at the apex; rachis and costae stramineous or occasionally the rachis tan, sparsely scaly, the scales ovate to lanceolate; veins free, not forked, 5–8(–10) per lobe; sori inframedial; indusial scale absent.

Additional specimens examined. BRAZIL. MINAS GERAIS: Serra de Babilonia (Minas), 6 Apr. 1868, *Glaziou* 2400 (P). PARANÁ: Serra do Mar, Volta Grande, 400 m, *Dusén* 725a (BM, GH, MO); Guaratuba, *Dusén* 13727 (GH). RIO DE JANEIRO: Organ Mountains, 29 May 1869, *Glaziou* 3333 (P). SANTA CATARINA: Meleiro, Araranguá, *Reitz* C 206 (US); Itacorubí, Florianópolis, *Reitz* 276 (US); Morro da Lagoa, *Rohr* 353 (US). SÃO PAULO: município Iguape, Peroupara, *Brade* 8250 (PH, UC); município Iguape, Serrinha, *Brade* 8343 (US). STATE UNKNOWN: no locality, *Müller* 1038 (US).

Stigmatopteris brevinervis is endemic to the coastal mountains of southeastern Brazil (Map 1); the only recorded elevation is 400 m. It closely resembles *S. tyucana*, the only difference being the degree of cutting. In *S. tyucana*, the pinnae are cut $\frac{1}{4}$ – $\frac{1}{2}$ to the costa; in *S. brevinervis*, the pinnae are cut $\frac{1}{2}$ – $\frac{2}{3}$ to the costa. *Stigmatopteris brevinervis* has a larger leaf and more pinnae than does *S. tyucana*, which suggests that *S. brevinervis*

may be merely a larger, more deeply cut form. Another difference is that *most* specimens of *S. tyucana* have medial to supramedial sori, whereas all those of *S. brevinervis* have inframedial sori. These two species are very similar and perhaps future study will show that they are conspecific.

2. *Stigmatopteris bulbifera* R. C. Moran, sp. nov. TYPE: Ecuador. Napo: Cerro Huacamayos, on road Baeza-Tena, ca. 34 km from Baeza, 2,000 m, Øllgaard *et al.* 35866 (holotype, AAU, 5 sheets). Figure 9. Map 1.

Folia 1-pinnata, pinnis 7–10 utroque costae latere, gemmis praesentibus in axillis pinnarum distalium; rhachis et costae abaxialiter glanduloso-pubescentes; venae irregulariter anastomosantes.

Rhizome short-creeping, the internodes 0.5–2 cm, the apex scaly, the scales 1–4 mm, lanceolate, dark brown, entire; leaves to 0.9–1.3 m; petioles nearly equaling the lamina, dull, brown, scaly, the scales 5–10 mm, lanceolate, brown, entire, not shiny adaxially; lamina 1-pinnate, oblong-deltate, buds usually present in the axils of the distal or medial pinnae; free pinna pairs 7–10; basal pinnae not reduced, widest near the middle, stalked, the stalk 2–5 mm; medial pinnae 18–25(–35) × 2.5–4.5(–6) cm, widest near the middle, the margins crenate-serrate or, in large leaves, cut $\frac{1}{2}$ to the costa; rachis and costae tan, puberulent and scaly, the hairs less than 0.1 mm, erect, capitate-glandular; veins partly free and partly anastomosing; sori discrete, round, lacking an indusial scale.

Additional specimens examined. COLOMBIA. CAQUETA: Putumayo, cerca de Buenosaires, 2,060 m, *Hageman & Leist 2072* (COL). CHOCÓ: between Pueblo Rico (Risardal) and Istmina (Chocó), along Quebrada Antón, 15 km W of Santa Cecilia, 240 m, *Croat 70911* (MO, UC). HUILA: Cordillera Oriental, Caquetá side of Huila-Caquetá divide, 20 km SE of Garzón, 2,380 m, *Little 9380* (COL, GH, US). MAGDALENA: Sierra Nevada de Santa Marta, finca Los Arroyitos, 1,600–1,700 m, *Kirkbride 2377* (COL). QUINDÍO: “Quindío” *Triana 615* (COL). ECUADOR. PICHINCHA: Saloya, road to Las Palmeras, mountain left of road across from Las Lagñas, 1,850 m, *Heinrichs 550* (F, Z).

Stigmatopteris bulbifera occurs in Colombia and Ecuador (Map 1), where it grows in wet forests from (240–)1,600 to 2,380 m. It resembles *S. heterophlebia* in that both are 1-pinnate, have anastomosing veins, and are beset with numerous capitate-glandular hairs on the abaxial surface of the axes. The two species are easily distinguished, however, by the characteristics given in the key. Other less constant characteristics are that *S. bulbifera* tends to be a much larger plant, with leaves

over one meter tall, and that *S. bulbifera* grows at higher elevations than *S. heterophlebia*. In general, *S. bulbifera* has a greater number of free veinlets per pinnae, sometimes up to 90% free. The buds are best seen on the adaxial side of the leaf.

3. *Stigmatopteris caudata* (Raddi) C. Chr., Bot. Tidsskr. 29: 302. 1909. *Polypodium caudatum* Raddi, Opusc. Sci. 3: 288. 1819. *Dryopteris caudata* (Raddi) C. Chr., Index Filic. 257. 1905. TYPE: Brazil. Rio de Janeiro: Gávea, Tijuca, *Raddi s.n.* (holotype, FI or PI not seen). Figure 10. Map 2.

Polypodium caudatum Kaulf., Enum. Filic. 113. 1824. TYPE: Brazil. Rio de Janeiro: *Mertens s.n.* (holotype, LZ—destroyed; isotype, C not seen; photos F, GH ex C).

Rhizome short-creeping; leaves to 2 m long; petiole $\frac{1}{2}$ to equaling the length of the lamina, brown, scaly, the scales 3–8 × 1–2.5 mm, lanceolate, brown, thin, lacking fibrillose scales; lamina 1-pinnate-pinnatisect, lanceolate, lacking buds, glands obscure; pinnae 15–32 × 4–7 cm, 15–20 pairs, cut $\frac{2}{3}$ – $\frac{7}{8}$ to the costa, sessile, the distal ones adnate with the basal basisopic lobe adnate to the rachis; lobes 3–8 cm wide, separated by broad, open, U-shaped sinuses, serrate on all sides, occasionally lobed, the basal basisopic segments reduced; rachis and costae tan to brown, scaly, the scales nonbullate, ovate, lanceolate; veins free, 9–15 per lobe, unbranched or 1-forked with a short acroscopic branch which (in fertile segments) bears the sorus; sori lacking an indusiumlike scale.

Additional specimens examined. BRAZIL. ESPÍRITO SANTO: Jatiboca, *Brade 18228* (NY). PARANÁ: município de Morretes, base do morro 7-astrada Graciosa, 1 m, *Dombrowski & Saito 1232* (US); Desvio Ypiranga, *Dusén 10341* (B, BM, US); Antonina, opp. Rio Demora, 200 m, *Dusén 14687* (BM, F, G, NY, US, Z); Serra do Mar, 580 m, *Jansson 740a* (F, G); município Paranaguá, Pico Torto, encosta oriental, 300 m, *Hatschbach 22873* (L, UC); município Morretes, Estr. Graciosa, Greta Funda, 500 m, *Hatschbach 24739* (NY, UC); município Guaraqueçaba, Rio do Custa, 50 m, *Hatschbach & Scherer 26665* (UC). RIO DE JANEIRO: Petropolis “Independencia,” *Alston & Lutz 289* (BM); Nouvelle Fribourg, *Claussen 133* (G, P); Palmeiras, *Preston s.n.* (K); Mt. Corcovado, 1815, *Cunningham s.n.* (BM, NY); Rio Corcovado, *Dusén 2538* (MO); Organ Mts., 1837, *Gardner 131* (K); Rio de Janeiro, 1822, *Gaudichaud s.n.* (B, F, G, K, P); Rio de Janeiro, *Glaziou 2396* (P), 6414 (B, P); Sebastianopol, *Martius s.n.* (B); alto Macahé, *Mendonca 1355* (B); Rio de Janeiro, *Miers s.n.* (B, BM, K, P); Rio de Janeiro, *Mosén 2694* (B); Rio de Janeiro, 1840, *Regnell 254a* (GH, NY, P); 1841, *Regnell 358* (US); near Rio de Janeiro, *Sello s.n.* (B, BM); brook trail between Paineiras and Jardim Botânico, 100–400 m, *L. B. Smith*

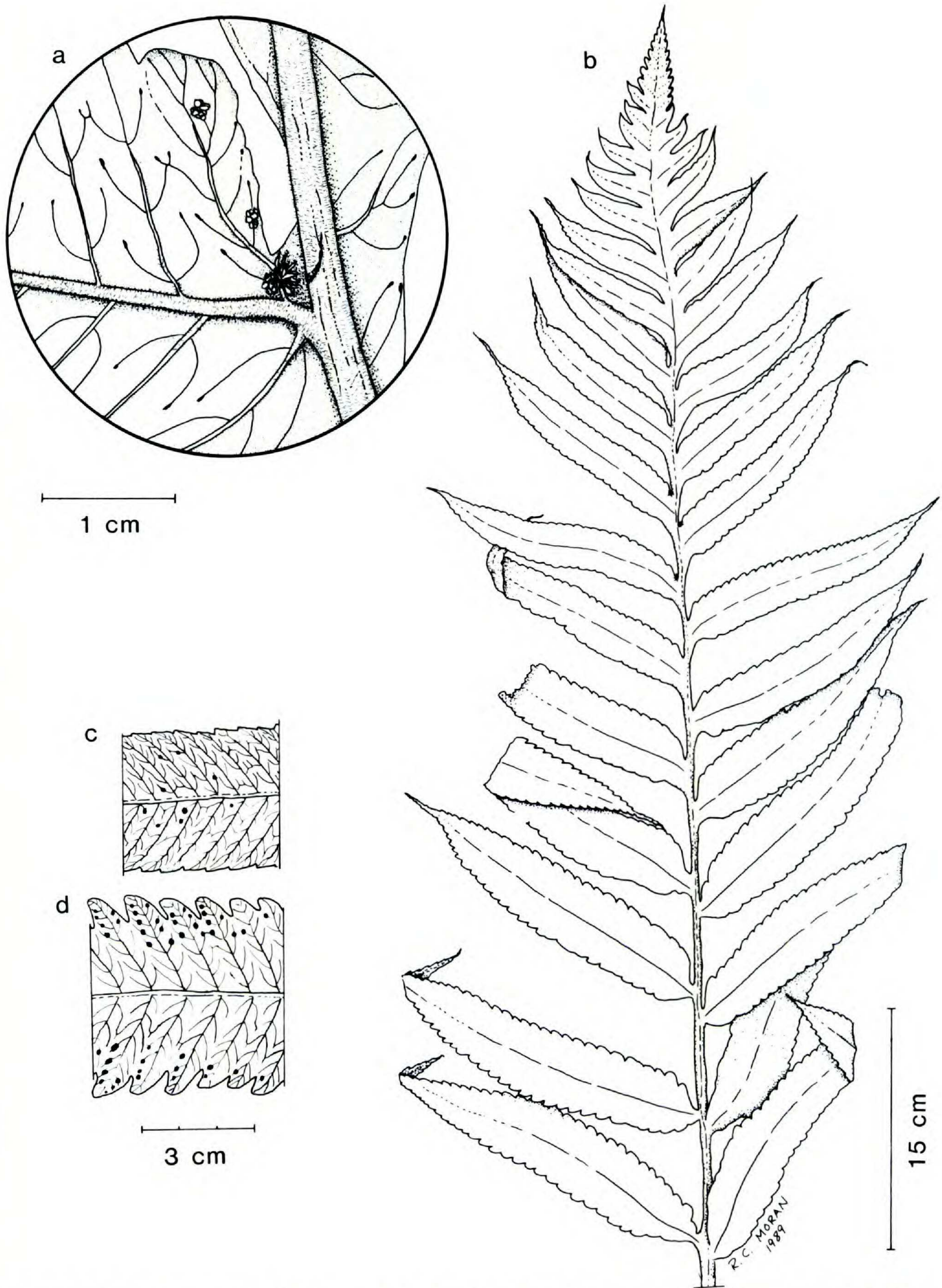


FIGURE 9. *Stigmatopteris bulbifera*. —a. Juncture of rachis and costa with bud (*Ølgaard et al.* 35866, AAU). —b. Lamina (*Heinrichs* 550, distal half, B; proximal half, F). —c. Part of fertile pinna (*Hageman & Leist* 2072, COL). —d. Part of fertile pinna (*Ølgaard et al.* 35866, AAU).

1391 (GH); near Rio de Janeiro, *U.S. Exploring Expedition* 23 (US); near Rio de Janeiro and Bahia, *Webb s.n.* (MICH, NY, US). SANTA CATARINA: município de Sombrio, Retiro, Araranguá, *Reitz* 227 (US); município de Meleiro, Araranguá, perto da cidade, *Reitz* C205 (US);

município de Brusque, Morro de Bateia, 100 m, *Reitz* 1909 (BM); município de Brusque, Ribeirão do Ouro, 600 m, *Reitz* 3542 (US); município de Ibirama, Horto Florestal I.N.P., 400 m, *Reitz & Klein* 3077 (US); município de Florianópolis, Sertão da Lagoa, *Rohr* 1072 (B, L, NY,

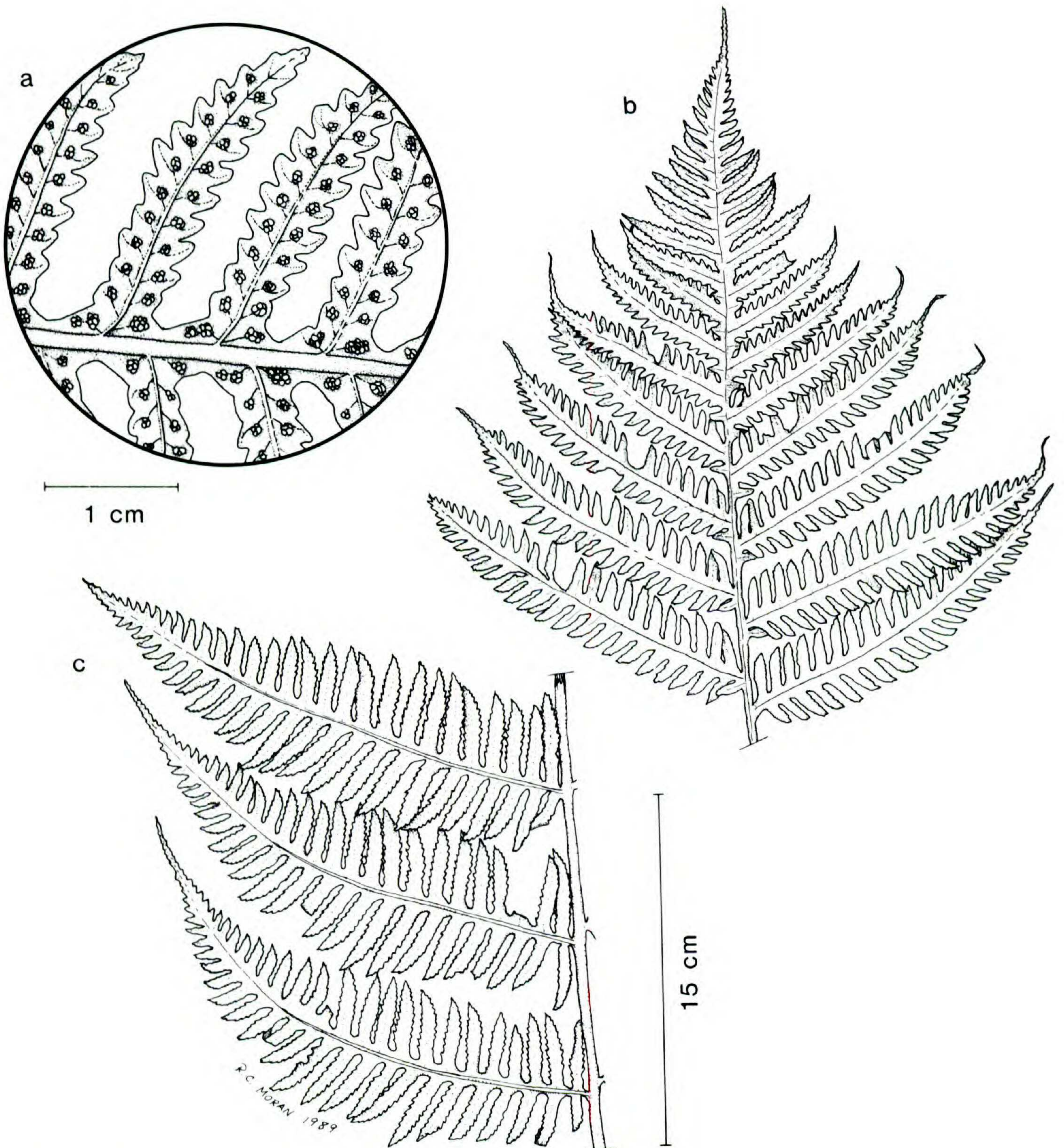


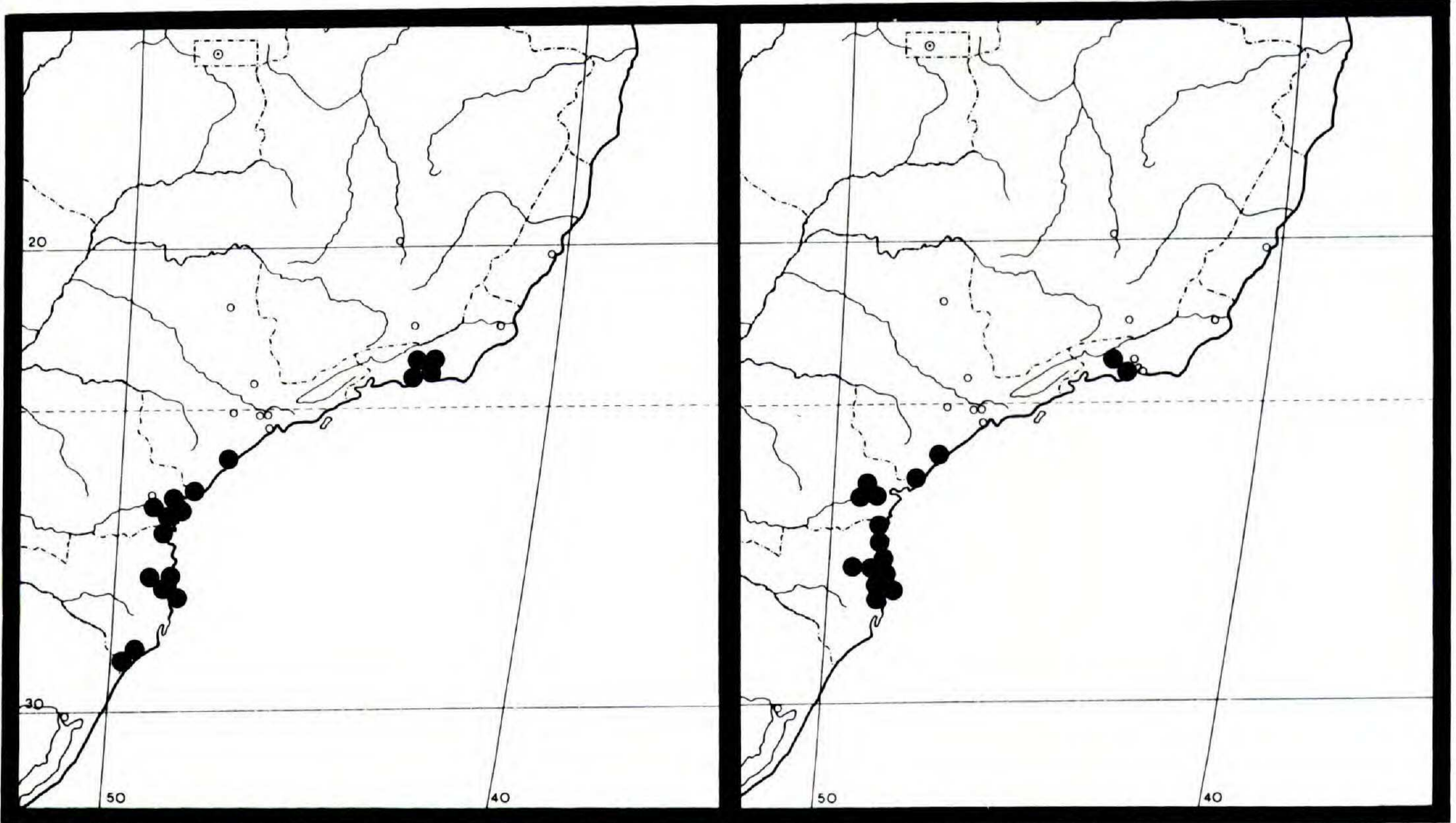
FIGURE 10. *Stigmatopteris caudata*. —a. Venation and sori. —b. Distal third of the lamina (Rohr 1072, US). —c. Basal pinnae (collector unknown, B).

US); município de Joinville, Schmalz 191 (F); Peninsula da Gloria, Feb. 1884, Ule 68 (K), 70 (P). SÃO PAULO: Iguape, Apr. 1922, Brade s.n. (US); Peroupara, Brade 8478 (NY, UC); Serra do Mar, Luederwaldt 21821 (GH); no locality, 1906, Wacket s.n. [Rosenstock, *Filices austrobrasilienses* no. 286] (B, GH, P, UC).

Stigmatopteris caudata is endemic to southeastern Brazil (Map 2) where it grows in wet forests from 0 to 600 m. It is the most highly cut species of *Stigmatopteris* in southeastern Brazil and has characteristic serrate segments separated by broad,

U-shaped sinuses (Fig. 10a). In its size and cutting, this species resembles *S. ichthiosma*, an Ecuadorian species, but differs by its more deeply serrate or lobed segments, wider sinuses, generally wider pinnae, and lack of an indusiumlike scale. The petiole scales also differ between the two species: *S. caudata* has thin scales, whereas at least some of those on *S. ichthiosma* are darkly sclerified adaxially.

Although I have not seen the type specimen of this species, I feel confident on the basis of Raddi's



MAP 2. Distribution of *Stigmatopteris caudata* (left) and *S. heterocarpa* (right).

original description and his later illustration (Raddi, 1825, fig. 39) that the name is here applied correctly.

4. *Stigmatopteris chimalapensis* Mickel & Beitel, Mem. New York Bot. Gard. 46: 356, fig. 129E, F. 1988. TYPE: Mexico. Oaxaca: Municipio Santa María Chimalapa, Cañada E de la vereda a La Gloria, ca. 8 km SE de Santa María, 350 m, *Hernández 1282* (holotype, NY). Figure 11.

Rhizome erect, short; leaf 70 cm; petiole equaling the lamina, brown to stramineous, sparsely scaly, the scales 1–3 mm, ovate to lanceolate, entire, appressed, shiny black abaxially; lamina 1-pinnate-pinnatifid, lanceolate, bulblets lacking; basal pinnae equilateral, widest at or slightly above the middle, short-stalked, the stalk 2 mm; medial pinnae 8–12 × 1.3–2 cm, equilateral, widest at the base, cut ca. ½ or slightly less to the costae, 14 pairs, sessile; lobes entire or slightly serrate at the apex, the proximal acroscopic ones elongated; rachis brown, costae stramineous, both axes scaly, the scales irregularly ovate to lanceolate, the margins ciliate; veins free, unbranched, 4–6 per lobe; sori lacking an indusial scale.

This species is known only from the type collection. It resembles *S. sordida*, with which it may eventually prove conspecific, but differs by its smaller size and less-cut pinnae.

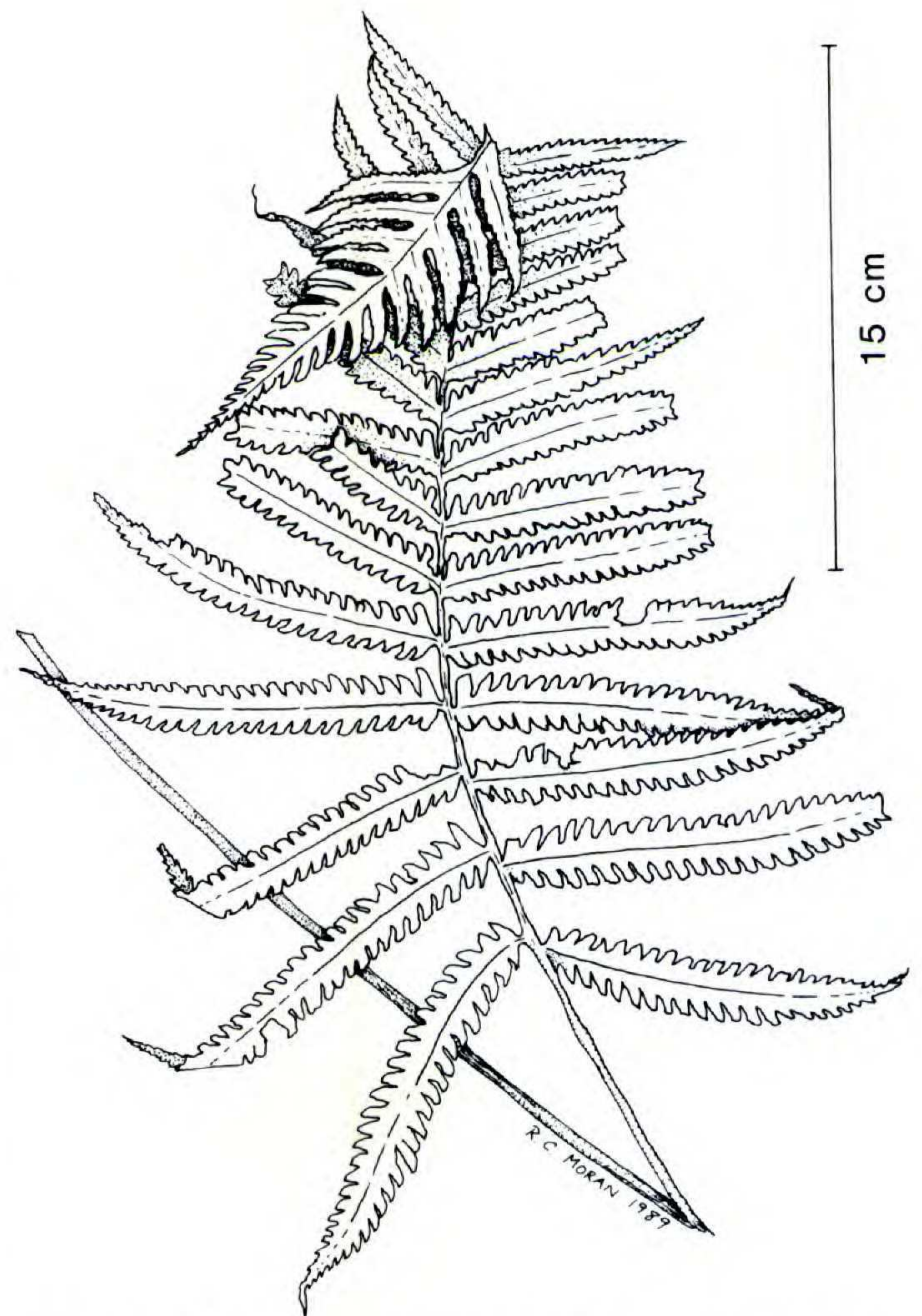


FIGURE 11. *Stigmatopteris chimalapensis*.—Leaf (*Hernández 1282*, NY).

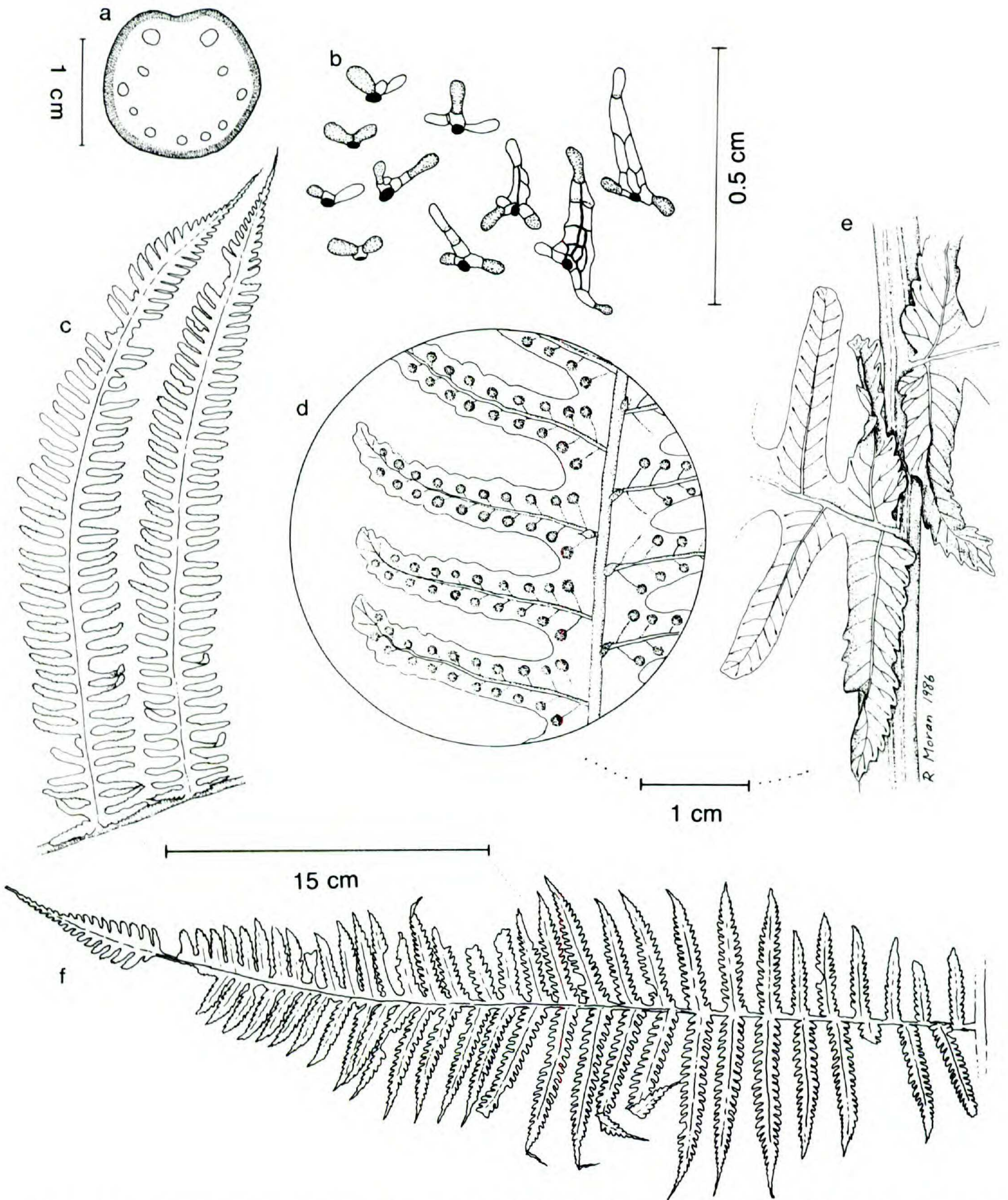


FIGURE 12. *Stigmatopteris contracta* (Moran 3187, MO).—a. Cross section of petiole base.—b. Proscasles or microscales (uniseriate) and multiseriate scales from the distal portions of the abaxial surface of the lamina.—c. Medial pinnae.—d. Venation and sori.—e. Segments of the pinna bases overlapping the rachis.—f. Large basal pinna.

5. *Stigmatopteris contracta* (Christ) C. Chr., Bot. Tidsskr. 29: 304. 1909. *Aspidium caudatum* var. *contractum* Christ, Bull. Herb. Boissier sér. 2, 6: 162. 1906. SYNTYPES: Costa Rica. Cartago: Navarro, 1905, 1,100 m, *Wercklé s.n.* (lectotype, here designated, P; isoelectotypes, BM, MICH, NY, US; photos,

GH, NY ex BM); Colombia (Nouvelle Granada), *Schlim 1683* (P—herb. Christ?, BM). (This specimen is here referred to *S. pellucidopunctata*.) Figure 12.

Rhizome up to 10 cm, erect or ascending; leaves 1–3 m; petiole $\frac{1}{2}$ – $\frac{3}{4}$ the length of the lamina,

brown, the scales 1–3 mm, ovate to nearly circular, opaque, appressed, dull brown adaxially, shiny black abaxially, these sometimes mixed with larger, thin, translucent, flaccid scales; lamina 80–200 × 40–95 cm, 1-pinnate-pinnatifid, lanceolate, bulblets lacking; medial pinnae 20–35 × 3–6 cm, linear, cut $\frac{3}{4}$ to nearly all the way to the costae, pairs 20–26, the base overlapping the rachis; basal pinnae 7–15 cm wide, elongated basiscopically, widest near the middle where the basiscopic basal segments are twice as long as the acroscopic ones; segments entire to crenate or serrate, the fertile ones contracted, their sinuses 1–2 times the width of the segments, U-shaped, the basal segments on both sides prolonged and overlapping the rachis; rachis brown; costae stramineous, scaly, the scales 1–2 mm, few, scattered, ovate, entire or nearly so, never fibrillose; veins free, 8–18 in the medial segments of the medial pinnae, those of the fertile segments unbranched, those of the sterile segments branched or unbranched; sori with indusial scale absent or rarely present, the scale ovate-lanceolate, borne on the basiscopic side, stipitate and held above the sporangia.

Additional specimens examined. COSTA RICA. ALAJUELA: canyon of Río Cariblanco and W slope and summit of ridge between Río Cariblanco and Quebrada Quicuyal, SW of Cariblanco, 840–950 m, *A. R. Smith et al.* 1862 (MO, NY, UC); Monteverde Cloud Forest Reserve, 1,250–1,350 m, *Burger et al.* 10735 (CR, F, NY, US); along road from San Ramón to Bajo Rodríguez, at Río Cataratas, *Croat* 68108 (MO, UC); Monte Verde Reserve, E slope of Cerro Centinelas, vicinity of Finca Peña Blanca, 1,300–1,400 m, *Grayum* 5374 (MO, UC, US); Univ. of San Ramón's Biological Field Station, 1,100 m, *Moran* 3187 (F, MO), 4126 (CR); N slope of ridge along quebrada draining E to Río Cataratas, ca. 20 km NW of San Ramón, 850 m, *A. R. Smith et al.* 2247 (CR, MO, UC); Reserva Forestal de San Ramón, Río San Lorenzito, 800–1,000 m, *Herrera et al.* 336, (MO, UC). CARTAGO: Pejivalle, *Lancaster* 836 (BM); El Muñeco, 1,400–1,500 m, *Standley & Torres* R. 51061 (US), *Stork* 2658 (UC, US); Navarro, 1,500 m, *Torres* 49 (US); without locality, *Endress* s.n. (K); 10 km SW of Navarro on a winding trail ca. 10 km S of Cartago and 1 km S of Finca Montecristo, 1,400–1,600 m, *White & Lucansky* 1968150 (DUKE, GH); Reserva de Tapantí, *Gómez* 1133 (CR), 2330 (CR, F, GH, MO, NY, US), 18905 (AAU, CR, MO, UC); forest near the entrance to Parque Nacional Tapantí, 1,270 m, *Moran* 3330 (CR, F, GH, MO, NY); along tributary of Quebrada Casa Blanca Tapantí, 1,350 m, *Grayum & Sleeper* 3714 (CR, MO, UC); slope N of Quebrada Casa Blanca, Tapantí, 1,350 m, *Grayum* 4570 (MO); ca. 22 km E of Turrialba, high ridge above Plantanillo, 1,200–1,450 m, *Mickel* 3430 (NY, UC, US); Turrialba, *Rojas G.* s.n. (CR); Platanillo, 650–900 m, *de la Sota* 5238 (US), *White & Lucansky* 1968174 (DUKE). HEREDIA: Virgen del Socorro, 1,000 m, *Moran* 3166 (MO), 1,500 m, *Wagner & Gómez* 79027 (CR); Cinchona, above the Upper Sarapaquí Valley, ca. 1,200 m, *Scamman* s.n. (GH). LIMÓN: Siquirres,

Stork 2263 (MICH). SAN RAMÓN: La Hondura, 1,000 m, *Nisman S.* 98 (GH), *Gómez* 281 (CR), 1,300–1,700 m, *Standley* 37834 (US); vicinity of La Hondura, 4 km S to 1 km N on Rte. 220, between Volcán Irazú and Volcán Barba, 1,250–1,500 m, *Mickel* 2241 (NY), 2249 (NY, UC, US). PANAMA. CHIRIQUÍ: Boquete, Dexter Trail, *Cornman* 1091 (F, GH, MICH, MO, UC); vicinity of El Boquete, 1,000–1,500 m, *Cornman* 914 (US); valley of the Río Piarnasta, ca. 5 mi. E of Boquete, 1,600 m, *Killip* 5159 (GH, MICH, MO, UC, US).

Stigmatopteris contracta grows from 650 to 1,600 m in the montane forests of Costa Rica and Panama. With leaves 1–3 m long, *S. contracta* is the largest species in the genus. The segments of the sterile and fertile leaves are subdimorphic, differing in width, cutting, and venation. The name *contracta* refers to the fertile segments, which are narrower than the sterile ones.

This species might be confused with large plants of *S. sordida*, which also grows in Costa Rica and Panama. *Stigmatopteris contracta* can be distinguished by its pinna bases that overlap the rachis, costal scales that are ovate and nearly entire, fertile segments that are contracted, and wide sinuses that are one to two times the width of the segments. A scalelike indusium is present on the type but absent from the other specimens.

I chose *Wercklé* s.n. as the lectotype because it preserves the previous usage of the species name, and it is more widely distributed in herbaria. The other syntype cited by Christ, *Schlim* 1683, is here referred to *S. pellucidopunctata*.

6. *Stigmatopteris gemmipara* C. Chr., Kongl. Svenska Vetenskapsakad. Handl. ser. 3, 16: 36, t. 9, figs. 5–7. 1937. *Dryopteris gemmipara* (C. Chr.) Maxon ex Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 26. 1953. TYPE: Haiti. Hotte, western group, stony ridge above La Mare Proux, near Torbec, 6 Dec. 1925, *Ekman* 5268 (holotype, S? not seen; isotype, IJ not seen). Figure 13.

Rhizome erect to decumbent, compact; leaves to 1 m; petioles equaling the length of the lamina, brown, scaly, the scales 0.5–1 cm, linear-lanceolate, brown, a few black, sclerotic, opaque; lamina 1-pinnate-pinnatifid, narrowly elongate-triangular to lanceolate, with buds in axils of distal pinnae, the apex attenuate; pinnae (4–)9–14 × (1.5–)2.5–3.5(–4) cm, 9–20 pairs, widest at or near the base, cut $\frac{1}{2}$ or more to the costa, the basal basiscopic segment occasionally free, reduced, the base of the proximal pinnae stalked, the stalk 4–6 mm; segments 4–6 mm wide at the middle, serrate, the apex obtuse, the basal basiscopic segment not ad-

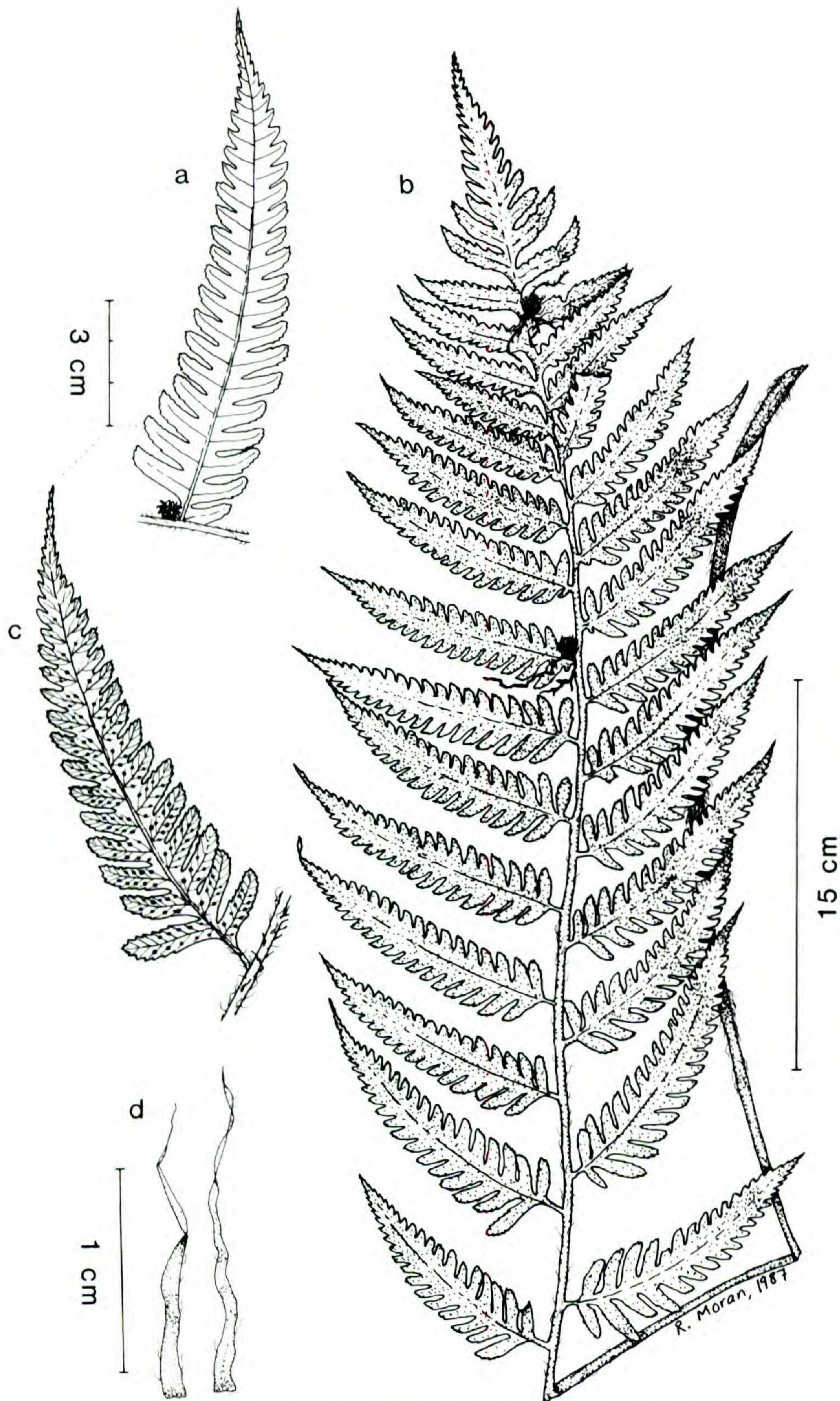


FIGURE 13. *Stigmatopteris gemmipara* (Ekman 10113, US). — a. Pinna with bud in axil. — b. Leaf with buds. — c. Fertile pinna, second from the base of b. — d. Petiole scales.

nate to the rachis; rachis and costae stramineous to light brown, scaly, the scales 2–3 mm, lanceolate to filiform, nonbullate, spreading, conspicuous, the costular scales nonbullate; veins free, mostly unbranched, 5–7(–8) per segment; sori lacking an indusiumlike scale.

Additional specimens examined. JAMAICA. PORTLAND: ca. 5 mi. SW of Priestman's River on the E

slope of John Crow Mts., ca. 500 m, *Proctor 4257* (US). HAITI. Massif de la Hotte, western group, Torbec, Morne Formon, *Ekman 7424* (BM, G, K, US); Massif de la Hotte, Les Roseaux, hab. Quillaud, 1,000 m, *Ekman 10113* (US).

Stigmatopteris gemmipara grows only in Jamaica and Haiti in woods over limestone soils from 500 to 1,200 m. This species could be confused

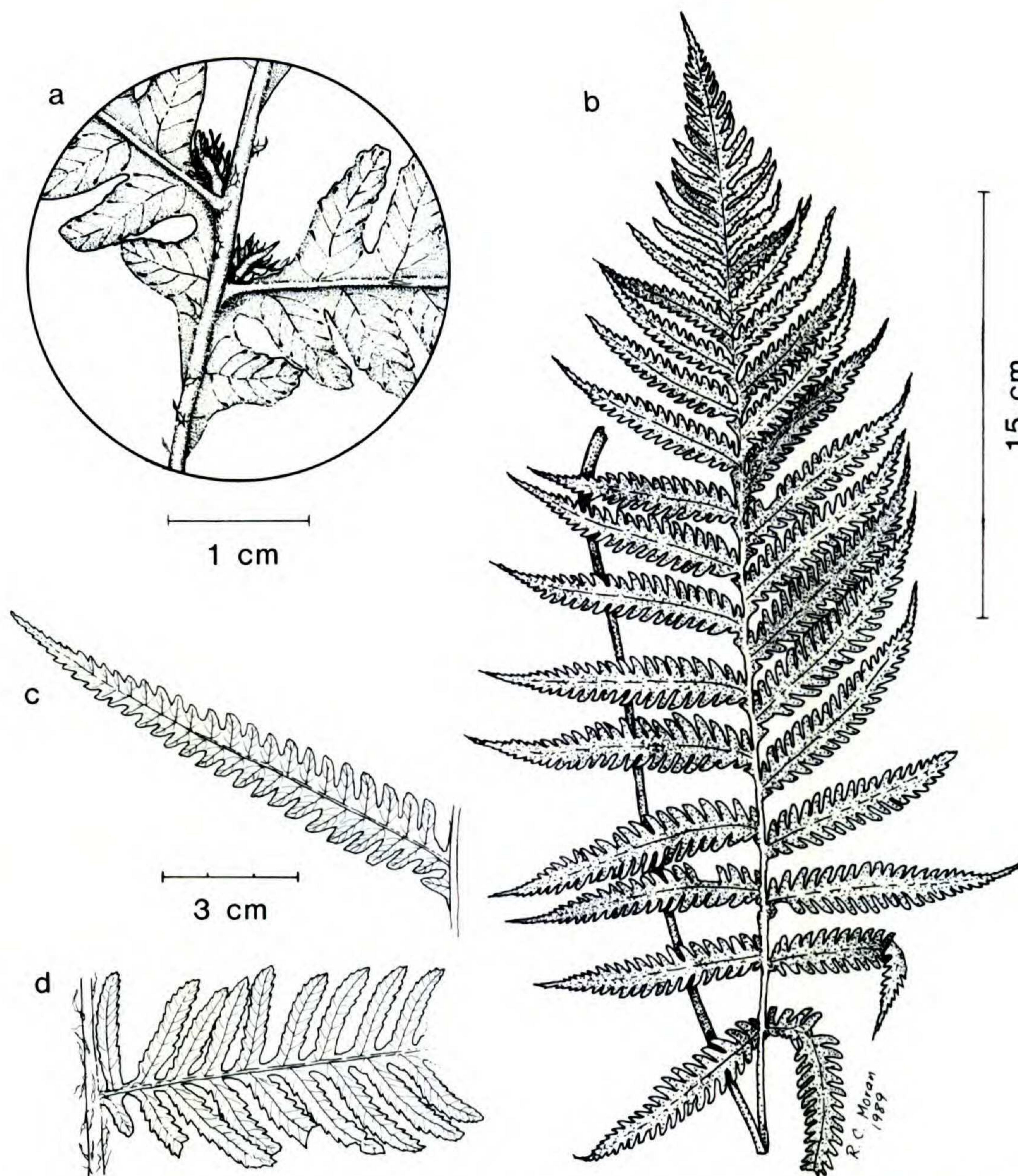


FIGURE 14. *Stigmatopteris hemiptera*.—a. Buds in the axils of distal pinnae; note that the basal basispic lobe is adnate to the rachis rather than to the costa (León *et al.* 10409, NY).—b. Leaf (Ekman 14356, GH).—c. Distal pinna (Ekman 14356, GH).—d. Proximal part of a large basal pinna (Wright 1053, US).

with *S. jamaicensis*, which is endemic to Jamaica, but that species lacks bulblets and has an indusiumlike scale subtending the sorus.

7. *Stigmatopteris hemiptera* (Maxon) C. Chr., Index Filic. Suppl. 3: 174. 1934. *Dryopteris hemiptera* Maxon, Contr. U.S. Natl. Herb. 24: 59. 1934. TYPE: Cuba, Sep. 1859–Jan. 1860, Wright 1053 (holotype, US; isotypes, BM, G, GH, K, MO, fragment B, US). Figure 14.

Rhizome decumbent, compact; leaves 45–130 cm long; petioles $\frac{1}{2}$ to equaling the lamina, stramineous to dull brown, sparsely scaly, the scales narrowly triangular, translucent or nearly so, not black and opaque; lamina 1-pinnate-pinnatifid, lanceolate, buds produced on small sterile leaves in the axils of the distal pinnae, the apex evenly

tapered; pinnae 11–18 \times 1.5–2.5 cm, 15–20 free pairs, widest below the middle, cut $\frac{1}{2}$ – $\frac{7}{8}$ to the costa, large plants occasionally with a free basal acroscopic pinnule, the base adnate in the distal $\frac{1}{2}$ of the lamina, with the basal basispic lobe arising from the rachis rather than the costa; segments 3–4 mm wide, the margins serrate, the apex rounded; rachis and costae stramineous, scaly, the scales scattered, nonbullate; veins 6–10 per segment, mostly unbranched; glands not easily visible; sori nonparaphysate, lacking an indusiumlike scale.

Additional specimens examined. CUBA. ORIENTE: Sierra Maestra, Loma del Gato, Clement 961 (GH, P, UC, US), 1,000 m, 1602 (Z); Hioram & Clement 6442 (GH, US); Sierra Maestra, on the divide below Río Yara and Río Palmamocha, ca. 1,000 m, Ekman 14356 (G, GH, NY, US); S side of the crest of the Sierra Maestra W of Aserraldero San Antonio de los Cumbres, region of La Bayamesa, 1,400–1,500 m, Morton 9569 (US); Loma

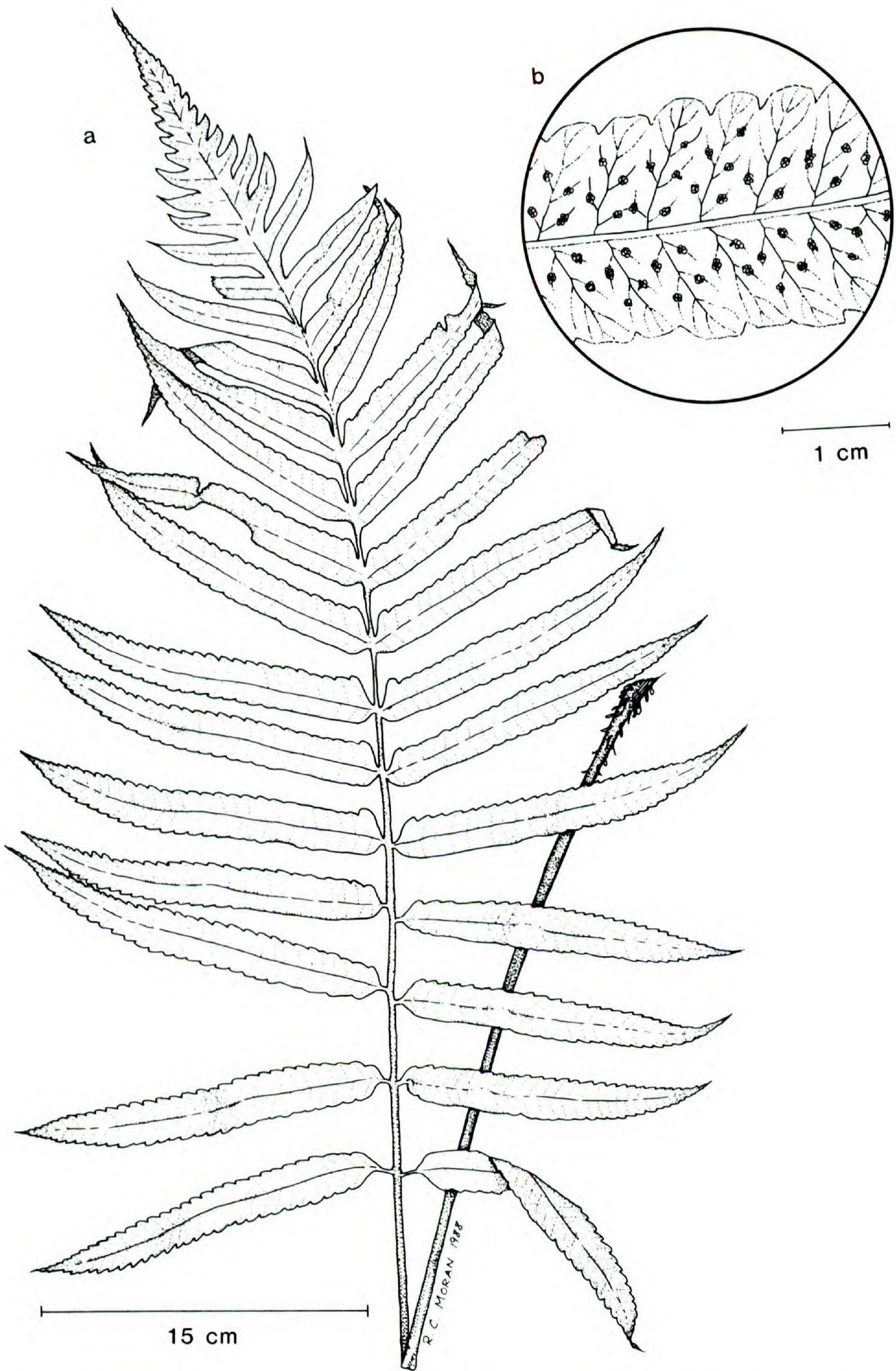


FIGURE 15. *Stigmatopteris heterocarpa* (Oliviera & Cordeiro 909, MO).—a. Leaf.—b. Venation and sori.

del Gato, *Ravins 961* (UC). SANTIAGO DE CUBA: Sierra Maestra, Loma de San Juan, near Loma del Gato, 1,000 m, *Clement 633* (NY), 900–950 m, *674* (P, US), 1,000 m, *945* (US), 1,000 m, *949* (P), *Fre. León et al. 10311* (US), *10409* (NY, US), *10486* (NY, US); Maestra Ridge, 1,300 m, *Fre. León 11133* (NY, US).

Stigmatopteris hemiptera is endemic to the Sierra Maestra mountains of eastern Cuba where it occurs in wet forests from 900 to 1,500 m. A diagnostic characteristic of this species is that the basal basiscopic lobes of the distal pinnae are adnate to the rachis, not the costae (Fig. 14a). Apparently, the buds are only on sterile leaves, unlike the closely related *S. gemmipara*, which has buds on the sterile and fertile leaves. This observation, however, should be confirmed by field studies, as there are few specimens of each species.

8. *Stigmatopteris heterocarpa* (Fée) Rosenstock, Repert. Spec. Nov. Regni Veg. 21: 347. 1925. *Phegopteris heterocarpa* Fée, Crypt. Vasc. Brésil 1: 100, t. 30, fig. 2. 1869. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro, *Glaziou 2401* (holotype, P; isotypes, K, P). Figure 15.

Polypodium carrii Baker in C. Martius, Fl. Bras. 1(2): 597. 1870. *Dryopteris carrii* (Baker) C. Chr., Index Filic. 257. 1905. *Stigmatopteris carrii* (Baker) C. Chr., Bot. Tidsskr. 29: 298. 1909. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro, *Carr s.n.* (holotype, K). *Stigmatopteris heterocarpa* var. *basilaris* Rosenstock, Repert. Spec. Nov. Regni Veg. 21: 347. 1925. TYPE: Brazil. São Paulo: município Iguape, Morro das Pedras, *Brade 8231* (holotype, S not seen; isotype, US).

Rhizome short-creeping; leaves to 1.5 m, petiole ca. equaling the lamina, stramineous to brown, scaly at the base, the scales 5–12 × 1–2 mm, brown, thin, lanceolate; lamina 1-pinnate-pinnatifid, lanceolate, lacking bulblets, only a few distal-most pinnae with short-decurrent bases; pinnae 14–23 × 1.7–3.2 cm, 12–17 pairs, nearly entire, crenate, or cut ¼ to the costa, the base sessile or nearly so, the basal pinnae short-stalked; lobes entire; rachis and costae stramineous, sparsely scaly, the scales ovate, lanceolate, or oblong; veins free, not forked, 3–5 per lobe; sori medial to inframedial; indusial scale absent.

Additional specimens examined. BRAZIL. MINAS GERAIS: Serra da Babilonia, 6 Apr. 1868, *Glaziou 2400* (P). PARANÁ: Desvio Ypiranga, *Dusén 8187* (BM, US); Porto de Cima, *Dusén 10244* (GH, NY, US), *14115* (B, GH), 200 m, *14680* (F, G, GH, NY, US); município Morretes, Estr. da Graciosa, Grota Funda, *Hatschbach 10748* (B, LIL), 500 m, *24376* (UC); município Tijucas do Sul, Rod. Br 468, Rio Itararé, 900 m, *Hatschbach*

25939 (NY, UC, US); município Morretes, Jurapê, *Hatschbach 41955* (UC, Z); município Morretes, Estação Marumbi, *Kummrow & Hatschbach 2536* (MU, UC, US); município Morretes, Vêu de Noiva, *Oliveira & Cordeiro 909* (MO, UC). RIO DE JANEIRO: Organ Mts., *Wagner 1402* (P). SANTA CATARINA: no locality, *Pabst 799* (B); Luis Alves, Itajai, *Reitz 206* (US); Antonio Carlos-Biguassú, *Reitz 259* (US); Fachinal, Biguaçu, *Reitz C919* (US); Luiz Alves, Itajai, *Reitz 1098* (G); Azambuja, Brusque, 50 m, *Reitz 1792* (US); Mata Hoffmann, Brusque, 50 m, *Reitz 3141* (US); Horto Florestal I.N.P., Ibirama, 500 m, *Reitz & Klein 3068* (US); Blumenau, *Schenck 494* (B); município Florianópolis, Sertão da Lagoa, *Rohr 392* (GH, US), *1006* (B, UC, US); Joinville, Dec. 1904, *Schmalz s.n.* [Rosenstock, Filices austro-brasil. exsicc. no. 106] (B, GH, NY, P, UC); Morro da Cruz, *Sehnem 808* (GH); Morro do Antão, 250 m, *Sehnem 3086* (B, US); município Brusque, Azambuja, Brusque, 35–135 m, *Smith & Reitz 6127* (US); Blumenau, *Spannagel 332* (US); São Francisco, Guli, *Ule 187* (P). SÃO PAULO: município Iguape, Morro das Pedras, *8510* (UC); Peroupara, *Brade 8473* (NY, UC), *8474* (NY, UC), *8476* (NY, UC); Ilha do Cardoso, Morro da Captação, en dirección al Morro dos Tres Irmãos, 180–570 m, Rio Perequê, *Forero et al. 8793* (COL); Blumenau, Paso Mansa, *Haerchen 106* [Rosenstock, Filices austro-brasil. exsicc. no. 106] (B, P, UC).

Stigmatopteris heterocarpa is endemic to southeastern Brazil, where it grows in wet forests from 50 to 900 m. It resembles *S. rotundata*, a species of the Lesser Antilles and northern South America, but differs by its fewer pinna pairs.

It is sometimes difficult to distinguish this species from *S. tyucana*, the only difference being that *S. tyucana* has pinnae more deeply cut and generally broader than does *S. heterocarpa*. Fieldwork coupled with cytological studies may provide further evidence as to whether these two species are truly distinct.

Rosenstock's var. *basilaris* was said to differ from typical *S. heterocarpa* only by its inframedial sori. This character intergrades with medial sori and is therefore not worthy of distinction.

9. *Stigmatopteris heterophlebia* (Baker) R. C. Moran, Fieldiana, Bot. n.s. 27: 45. 1991. *Polypodium heterophlebium* Baker, J. Bot. 22: 363. 1884. *Dryopteris heterophlebia* (Baker) C. Chr., Index Filic. 270. 1905. TYPE: Costa Rica. Province unknown: Laguna, 305 m, *Harrison 59* (holotype, K). Figure 16. Map 3.

Rhizome short-creeping, the internodes 0.5–1 cm, the scales 1–3 mm, ovate to lanceolate, opaque, black, rigid, entire; leaves 45–100 cm; petiole ca. equaling the lamina, dull brown or tan, puberulent, scaly, the scales of two types, the first type 2–5 mm, opaque, appressed, shiny black adaxially, en-

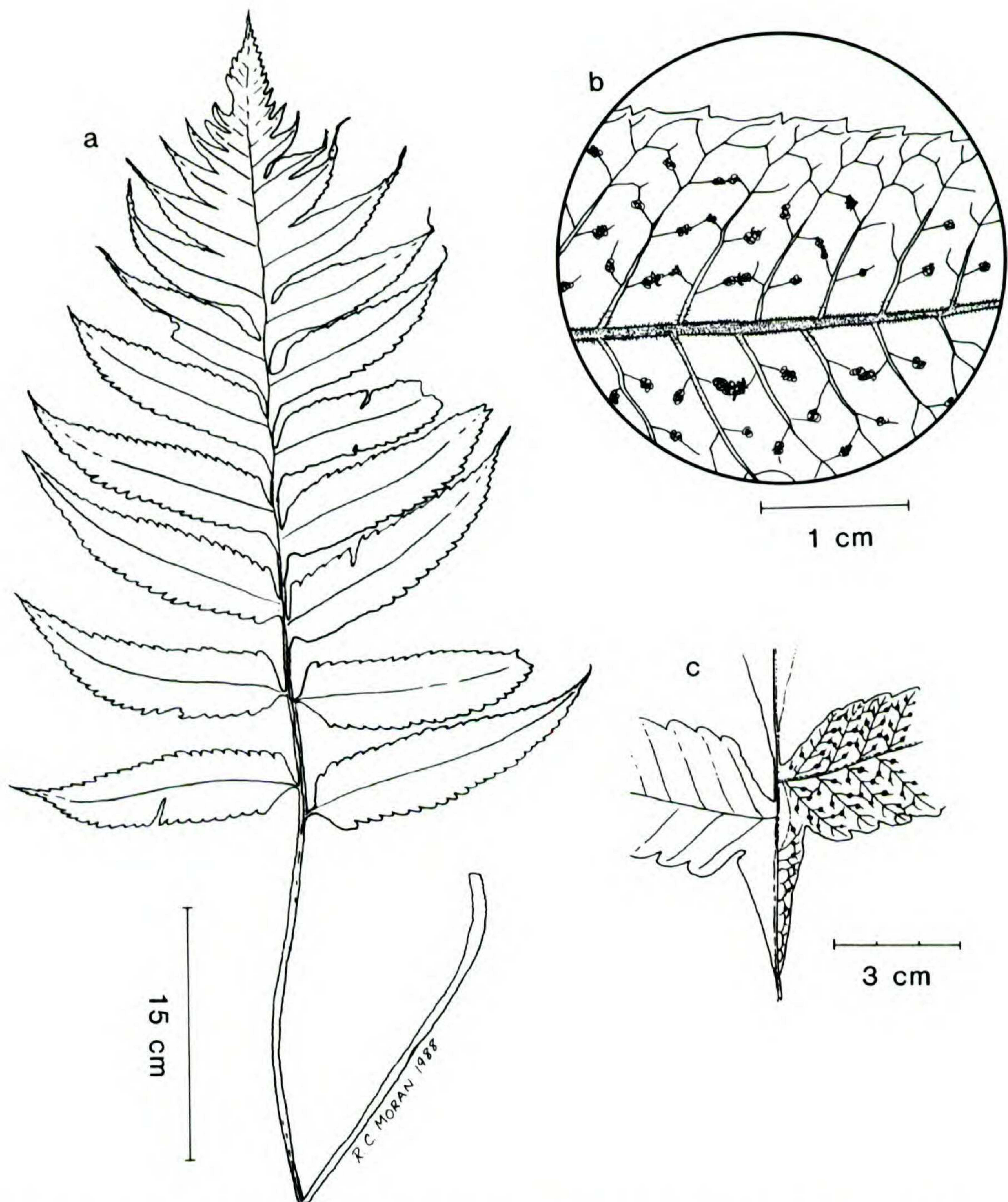


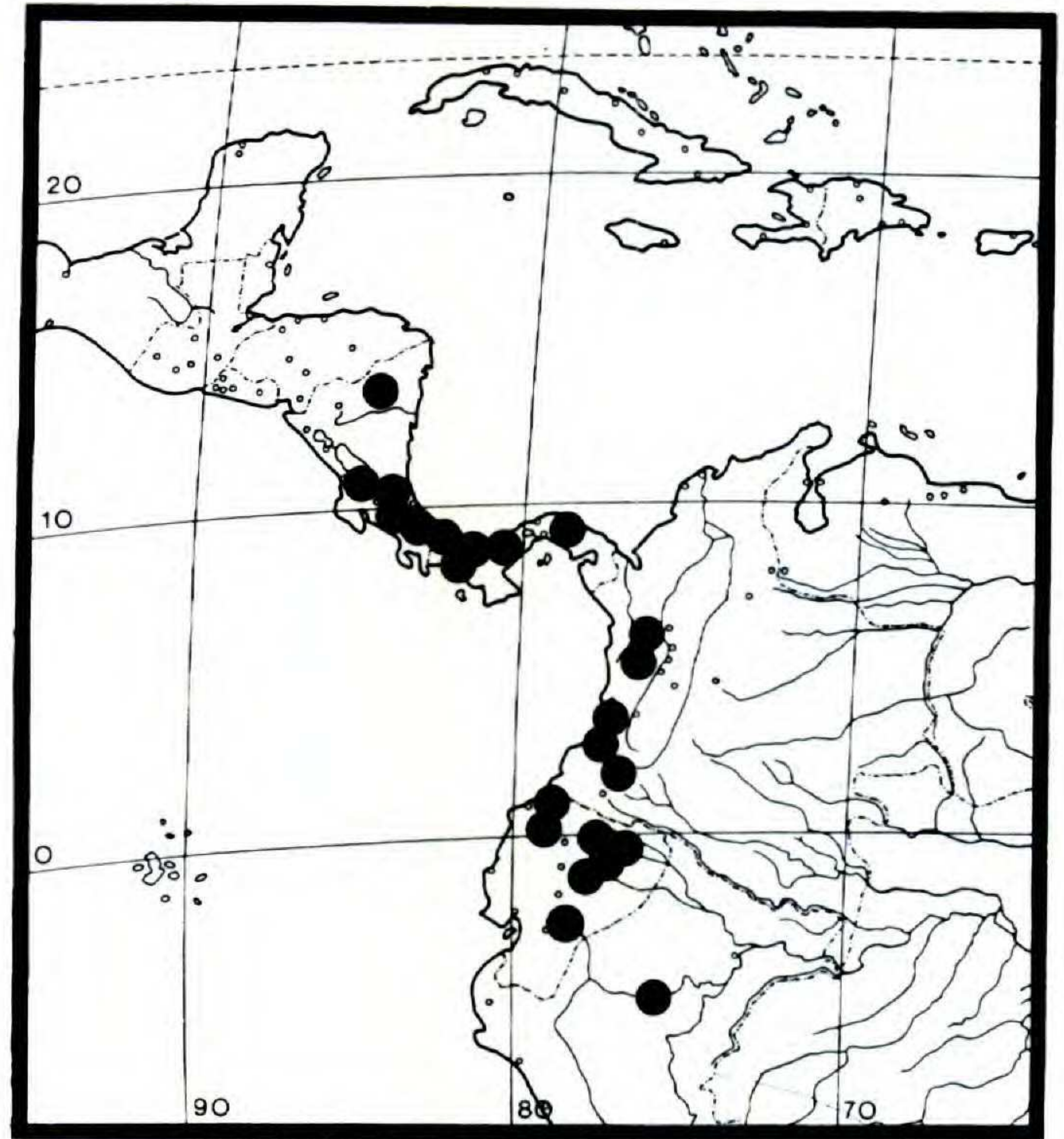
FIGURE 16. *Stigmatopteris heterophlebia*. —a. Leaf (Moran 3613, MO). —b. Sori and irregularly anastomosing veins. —c. Decurrent pinna bases (redrawn from Christensen, 1909).

tire, ovate-lanceolate, slightly falcate, the second tire 4–9 mm, translucent, spreading, brownish, lanceolate; lamina 1-pinnate, oblong-deltate to lanceolate, buds lacking or rarely (in NW Ecuador) present; free pinna pairs 1–3(–4); basal pinnae usually somewhat reduced, widest near the middle, stalked, the stalk 2–4 mm; medial pinnae (or lobes) 10–16(–18) × 2.5–3.5(–5) cm, widest at or near the base, the margins entire to crenate, the base adnate and decurrent to or nearly to the next pinna pair; rachis and costae tan, light brown, or stramineous, puberulent and scaly, the hairs less than 0.1 mm, dense, erect, capitate-glandular (when fresh), the scales to 3 mm, lanceolate, not fibrillose; veins part free and part anastomosing; sori discrete

or confluent where the veins anastomose, indusial scale absent.

Additional specimens examined. NICARAGUA. ZELAYA: Cerro Saslaya, 20 km W of Siuna, 1,100–1,400 m, Neill 1886 (CR), 3826 (CR, MO). COSTA RICA. ALAJUELA: Reserva Forestal de San Ramón, 800–1,200 m, Herrera Ch. et al. 162 (MO, UC), 316 (AAU, MO, NY, UC, US); canyon of Río Cariblanco and W slope and summit of ridge between Río Cariblanco and Quebrada Quicuyal, SW of Cariblanco, 840–950 m, A. R. Smith et al. 1876 (CR, MO, UC); Univ. of San Ramón's Biological Field Station, ca. 20 km N of San Ramón, along the Río San Lorencito, 800–900 m, Moran 4130 (CR, MO, UC); Upala, falda sur de Volcán Miravalles, Chacón s.n. (CR); Bajos de Jamaical Reserva de San Ramón, 700–1,000 m, Chacón 1776 (CR); Colonia Virgen del Socorro, Sarapiquí, Ocampo S. 1029 (CR); above San Ramón on road

to Los Angeles Norte, ca. 30 km above San Ramón, 610 m, *McAlpin 1313* (DUKE), *1326* (DUKE); Reserva de Monteverde, vertiente Pacífico, 1,520–1,580 m, *Dryer 369* (F); ca. 20 km NW of San Ramón, ca. 850 m, *A. R. Smith et al. 2253* (CR, MO, NY, UC); Univ. of San Ramón's Biological Field Station, *Moran 3188* (CR, F, GH, MO); 11 km N of San Ramón, 1,000 m, *Mickel 2955* (NY, UC, US); Univ. de Costa Rica Reserva, Fila Volcán Muerte, above the headwaters of the Río San Lorenzo, 1,000–1,300 m, *Barringer & Gómez-Laurito 2583* (F). CARTAGO: Peralta, *Lankester 893* (BM, US); SE of Turrialba, ca. 3 km NE of La Suiza, 1,200 m, *Lellinger & White 1412* (CR, F, US); SE of Orosi, ca. 2.2 km SSE of Purisil, above Finca La Concordia, 1,800 m, *Lellinger & White 1476* (MICH, MO, US); Turrialba, 600 m, *Gómez 987* (CR); near Turrialba, slope of the Río Reventazón behind the Instituto Interamericano de Ciencias Agrícolas, 600 m, *Mickel s.n.* (UC); along trail leading E into mountains from road into Tapantí Reserve ca. 1 km S of jct. of Quebrada Salto and Río Grande de Orosi, 1,500–1,800 m, *A. R. Smith 2121* (CR, UC); San Juan del Norte, 1,066 m, *Scamman 7667* (GH, US); 3 km W of Turrialba, 750 m, *Mickel 2622* (NY, US); ca. 22 km E of Turrialba, high ridge above Platanillo, 1,200–1,450 m, *Mickel 3447* (NY); El Muñeco, 1,400 m, *Stork 2722* (US); El Muñeco, on the Río Navarro, 1,400–1,500 m, *Standley & Torres R. 51069* (US); Tapantí Reserve, 1,400–1,700 m, *Gómez 19288* (AAU, MO, UC). GUANACASTE-ALAJUELA: slopes of Miravalles, above Bijagua, ca. 1,500 m, *Gómez et al. 19173* (AAU, MO, UC). HEREDIA: Virgen del Socorro, 1,000 m, *Moran 3165* (F, MO, NY), *Wagner & Gómez 79021a* (CR); forest between Río Peje and Río Sardinalito, Atlantic slope of Volcán Barva, 700–750 m, *Grayum 6651* (MO, UC); between Quebrada Tigre and E fork of Río Sardinal, ca. 9 km SW of Las Horquetas, ca. 600 m, *Grayum et al. 5043* (CR, MO, UC); Tirimbina, 213 m, *Proctor 32327* (F, MO); Cerro Gallito, 1,800 m, *Valerio 295* (US); S slopes of Cerro Zurquí, 5 km N of San Luis Norte, 1,800 m, *Stolze 1634* (CR, F, UC, US). LIMÓN: vic. of Guápiles, 300–500 m, *Standley 37169* (GH, US); along Río Costa Rica, SW of Guápiles, 300 m, *Grayum et al. 3288* (MO, UC). PUNTARENAS: Monte Verde Reserve, Sendero Brillante, 1,500 m, *Hammel & Zuchowski 13880* (MO). SAN JOSÉ: La Palma, 1,400 m, *Brade 481* (GH, NY, UC); Estación Carrillo de 700 a 450 m de la Fila al Cañón del Río Sucio, *Chacón & Herrera 1624* (CR, MO, UC); Parque Nacional Braulio Carrillo, Estación La Montura, 1,050 m, *Gómez et al. 20858* (CR, MO, UC, US); Zurquí, 1,900 m, *Gómez 3522* (CR); along unnamed N fork of Río Zurquí, ca. 1,500–1,600 m, *A. R. Smith 1692* (NY, MO, UC). PROVINCE UNKNOWN: 1901–1905, *Wercklé s.n.* (NY, US). PANAMA. BOCAS DEL TORO: Oleoducto Road, near Continental Divide, Fortuna Dam area, 1,000 m, *Churchill et al. 4549* (MO, UC); Cerro Colorado, ca. 8.6 mi. W of Chamé, *Croat 69137* (MO, NY, UC); along road between Fortuna Dam and Chiriquí Grande, 7.3 mi. N of bridge over Fortuna Dam, 3.2 mi. N of Continental Divide, 700 m, *Croat & Grayum 60216* (MO, UC), *60217* (AAU, MO, UC); vic. of Fortuna Dam, below pass on Chiriquí Grande road, ca. 800 m, *McPherson 9730* (MO); road from Fortuna Dam to Chiriquí Grande, 3.1 mi. N of Continental Divide, 700 m, *McPherson 6774* (MO, UC). CHIRIQUÍ: El Boquete, 1,000–1,500 m, *Cornman 1180* (US), *1210* (MICH, MO, UC, US), *1284* (US); La Fortuna hydroelectric project, 1,300–1,400 m, *Hammel 2227* (AAU, CR, MO); Fortuna Dam area, N



MAP 3. Distribution of *Stigmatopteris heterophlebia*.

of reservoir, Quebrada Bonito to E of road, 1,100 m, *Churchill 5255* (MO); vic. of Cerro Colorado, above San Felix, 1,450 m, *McPherson 12677* (MO); Dpto. Boquete, Fortuna dam site, along trail following Continental Divide, 1,100 m, *van der Werff & van Hardeveld 6762* (MO, NY, UC); along road between Fortuna Lake and Chiriquí Grande, 4.5–5 km N of dam over Fortuna Lake, 1,100–1,135 m, *Croat & Grayum 60043* (MO); along road between Gualaca and Fortuna Dam site 7.9 mi. beyond (NW of) Los Planes de Hornito, 1,300 m, *Croat 49916* (MO); vic. of Fortuna Dam in valley of Río Chiriquí, along aqueduct trail for water supply to IRHE facilities, 1,100–1,200 m, *Croat 66559* (AAU, MO, NY, UC); valley of the Río Piarnasta, ca. 5 mi. E of El Boquete, 1,525–1,600 m, *Killip 5387* (F, UC, US). COCLÉ: valle de Antón, 1,000 m, *Alston 8745* (BM, MO). PANAMÁ: trail from end of road past Los Altos de Pacora region of Cerro Jefe, on to Cerro Brewster, 600–800 m, *Hammel & de Nevers 13578* (MO, UC). VERAGUAS: 3 mi. from Escuela Agrícola Alto Piedra on road to Río Calovébora, 731 m, *Antonio 2050* (CR, MO); valley of Río Dos Bocas on road between Alto Piedra (above Santa Fé) and Calovébora, 350–400 m, *Croat 27477* (MO, NY); on Caribbean slope above Río Primero Brazo, 5 mi. NW of Santa Fé, 700–1,200 m, *Croat & Liesner 1010* (MO). COLOMBIA. CAUCA: Coteje, Río Timbiqui, *Lehmann 8951* (F, GH, K, US); Cordillera Oriental, comisaria of Putumayo, Oreto (Indian pueblo) on Río Oretopungo, tributary of Río Putumayo, 450 m, *Ewan 16775* (BM, UC, US). CHOCÓ: Municipio de San José del Palmar, hoyo del Río Torito, afluente del Río Hábita, 850–950 m, *Forero et al. 7407* (MO); Carretera Ansermanuevo–San José del Palmar, entre el Alto del Galapago y San José del Palmar, 1,900 m, *Forero et al. 2309* (COL, MO). EL VALLE: Costa del Pacífico, Río Cajambre, San Isidro, 5–100 m, *Cuatre-casas 17336* (US). ECUADOR. ESMERALDAS: banks of Río Palaví, 0.5 km below Awá encampment, 100 m, *Hoover et al. 4304* (MO, UC), *4325* (MO, UC). MORONA-SANTIAGO: along new road Méndez–Morona, 650 m, *van der Werff & Gudiño 11125* (MO, UC). NAPO: Añangu, Parque

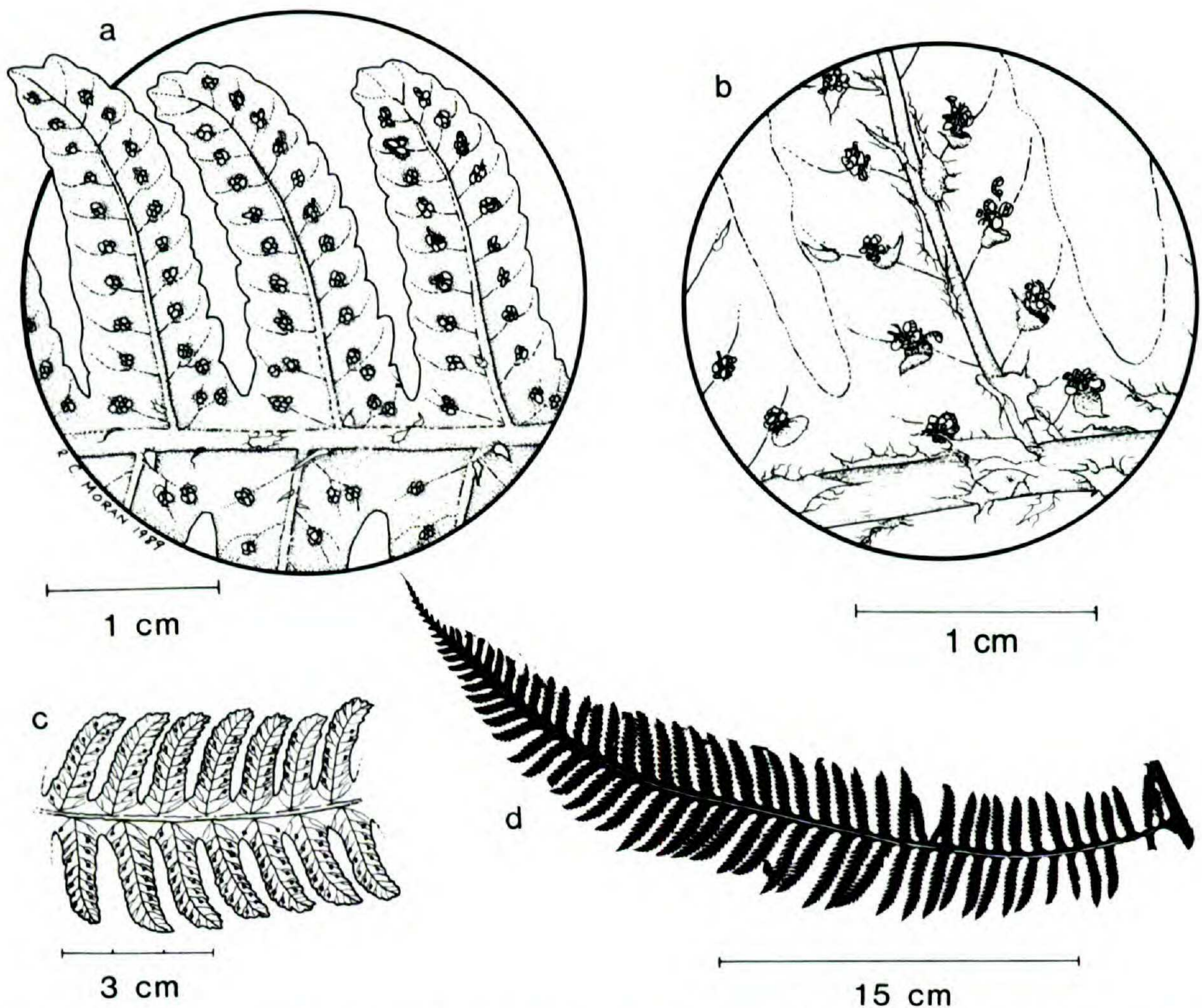


FIGURE 17. *Stigmatopteris ichthiosma*.—a. Sori and venation.—b. Sori subtended by indusiumlike scale and lanceolate scales on the costa.—c. Medial portion of pinna.—d. Large basal pinna. a–c, Cazelet & Pennington 5276, UC. d, Sodiro s.n., P.

Nacional Yasuní, 260–350 m, Ølgaard *et al.* 39229 (AAU); 12 km SW de Coca, por el camino se llama Los Zorros, 240, Moran 3613 (MO); Estación Experimental de INIAP, San Carlos 6 km al SE de Los Sachas, 250 m, Baker 5934 (NY); at Río Payamino 60 km along Río Payamino W of Coca, 350 m, Holm-Nielsen & Jeppesen 811 (AAU, GH). PICHINCHA: NE of Vicente Maldonado, Reserva de ENDESA, 600 m, Laegaard 51611 (AAU, MO). PERU. LORETO: Santa Rosa, lower Río Huallaga below Yurimaguas, ca. 135 m, Killip & Smith 28984 (NY, US).

Stigmatopteris heterophlebia occurs from Nicaragua to Peru (Map 3) in wet forests from 100 to 1,900 m. It resembles *S. bulbifera* in its glandular hairs that densely cover the axes but differs from that species by its few free pinna pairs. A further difference is that *S. heterophlebia* usually lacks buds, whereas *S. bulbifera* has them on the adaxial surface of the rachis—costae junctures. This characteristic is not completely constant because two specimens of *S. heterophlebia* from the department of Esmeraldas, Ecuador, have buds.

This species is also variable in the scaliness of the axes. Several specimens from Costa Rica and Panama (Hammel & de Nevers 13578, Lellinger & White 1692, Croat & Liesner 1010) are ex-

tremely scaly but are typical in all other characteristics, and no other feature seems to correlate with the scaliness.

Stigmatopteris heterophlebia has been previously called *S. alloëoptera* (Kunze) C. Chr., a name that cannot be used because it is of uncertain application (see section on names of uncertain application).

10. *Stigmatopteris ichthiosma* (Sodiro) C. Chr., Bot. Tidsskr. 29: 302. 1909. *Polypodium ichthiosmum* Sodiro, Recens. Crypt. Vasc. Quit. 59. 1883, as *ichtiosmum* in Sodiro, Crypt. Vasc. Quit. 294. 1893. *Dryopteris ichthiosma* (Sodiro) C. Chr., Index Filic. 271. 1905. TYPE: Ecuador, "Atcao, 1,500 m, S. Florencia, etc." Sodiro s.n. (holotype, Q; isotypes, BM, K, P). Figure 17.

Polypodium dentatum Baker, Ann. Bot. (London) 5: 456. 1891, nom. illeg., not Forssk. 1775. *Dryopteris longipetiolata* C. Chr., Index Filic. 275. 1905, nom. nov. for *P. dentatum* Baker. TYPE: Ecuador. "Andes of Ecuador," Sodiro s.n. (holotype, K).

Rhizome short-creeping; leaves to 2 m long;

petiole $\frac{1}{2}$ to equaling the length of the lamina, brown, scaly, the scales $4-6 \times 2-2.5$ mm, ovate, symmetrical, occasionally with darkly sclerified abaxial surfaces, the base cordate (appearing false-peltate), fibrillose scales absent; lamina 1-pinnate-pinnatifid, lanceolate, lacking bulbils; pinnae $20-40 \times 2.5-6$ cm, 15-20 pairs, cut ca. $\frac{2}{3}$ to the costa, sessile or the basal ones short-stalked, the stalk 2-7 mm; segments 4-10 mm wide, serrate at the apex, the sides entire, serrate or rarely lobed, basal basisopic segment not reduced; rachis and costae stramineous or brown, scaly, the scales non-bullate, ovate, lanceolate, or filiform; veins free, 7-14 per segment, unbranched or 1-forked with a short acroscopic branch which in fertile segments bears the sorus; sori with an indusiumlike scale.

Additional specimens examined. ECUADOR. CHIMBORAZO: red bark woods of Chimborazo, Río Chasnan, *Spruce 5714* (BM). PICHINCHA: "Andes of Quito," *Sodiro s.n.* (AAU, P, Q); Toachi, Sep. 1874, *Sodiro 48/1* (K); 20 km W of Santo Domingo de los Colorados, 300 m, *Cazelet & Pennington 5276* (NY, UC, US); road Chillogallo-Santo Domingo below Chiriboga, 16 km from the new road, 1,600 m, *Holm-Nielsen et al. 24819* (AAU); Maquipucuna Biological Field Station, ca. 5 km S of Nanegalito and ca. 25 km N of Quito, 1,400-1,700 m, *Moran 5250* (MO, QCNE); 2.5 km E of Cornejo Astorga, 1,200 m, *Moran 3545* (MO, Q, QCA). PROVINCE UNKNOWN: near Río Blanco, 1,800 m, *Mille s.n.* (P); near Angamarca, 12/905, *Sodiro s.n.* (P); no location, *Stübel 797* (B).

Stigmatopteris ichthiosma occurs in the western Andes of Ecuador in wet forests from 300 to 1,800 m. It resembles *S. pellucidopunctata* in leaf shape and cutting, but differs by its ovate to lanceolate (rather than filiform) scales on the abaxial surface of the axes, ovate (rather than lanceolate-falcate) petiole scales, and the presence of an indusiumlike scale that subtends the sorus (rather than none). Furthermore, *S. ichthiosma* occurs only in the western Andes, whereas *S. pellucidopunctata* occurs only on the eastern side of the Andes.

The specific epithet is usually spelled *ichtiosma*; however, Sodiro's (1883) original spelling is *ichthiosma*. He later altered it to *ichtiosma* but did not give a reason (Sodiro, 1893). According to Sodiro (1883), the dried plant smells like fish, thus the specific epithet from the Greek *ichthys*, fish, and *osme*, odor. I prefer to maintain the original spelling because its derivation is clear and because Article 73.1 of the *Code* (Greuter et al., 1988) states that the author's original spelling should be maintained. I cannot, however, detect a fishlike odor from the dried plants.

Christensen (1909, 1913) listed this species from

Cuba and Jamaica; however, the specimens he cited represent two closely related species: *S. hemiptera* (Maxon) C. Chr. (endemic to Cuba) and *S. jamaicensis* (Desv.) Proctor (endemic to Jamaica).

The other Ecuadorian specimens collected by Sodiro (see specimens examined) might also be types, because he says "etc." for the type localities, meaning other sites on the western slopes of the Andes.

11. *Stigmatopteris jamaicensis* (Desv.) Proctor, Brit. Fern Gaz. 9: 221. 1965. *Cystopteris jamaicensis* Desv., Mém. Soc. Linn. Paris 6: 263. 1827. TYPE: "Habitat in Antillis" [undoubtedly Jamaica], *Tussac s.n.* (holotype, P; photos, BM, GH, UC, US ex P). Figure 18.

Dryopteris nothochlaena Maxon, Contr. U.S. Natl. Herb. 24: 58. 1922. *Stigmatopteris nothochlaena* (Maxon) C. Chr., Index Filic. Suppl. 3: 174. 1934. TYPE: Jamaica. St. Thomas: near Cuna Cuna Pass, 610-823 m, *Maxon 1738* (holotype, US).

Rhizome erect, compact; leaves to 2 m long; petioles ca. $\frac{1}{2}$ the length of the lamina, stramineous to brown, glabrate to densely scaly (especially toward the base), the scales 1-1.5 cm, spreading, ovate-lanceolate; lamina 1-pinnate-pinnatisect, or fully 2-pinnate at the base, oblong to lanceolate, lacking buds; pinnae $15-23 \times 2-4(-5)$ cm, 22-26 pairs, widest at or below the middle, cut $\frac{7}{8}$ to nearly to the costa, the base sessile or nearly so; segments 3-7 mm wide, serrate, the apex rounded; rachis and costae stramineous, scaly, the scales ovate to lanceolate, those of the costules bullate; veins free, 8-11 per segment, mostly simple, not forked, scaly, the scales ovate, bullate; sori covered by an indusiumlike scale similar to those on the veins.

Additional specimens examined. JAMAICA. CLARENDON: Second Breakfast Spring, below Tweedside, 610 m, *Underwood 1613* (NY, US); Tweedside, *Harris 7419* (BM, NY), *Underwood 2036* (NY). PORTLAND: Mabess River, E bank, Blue Mts., *Papenfuss s.n.* (UC); Mabess River, ca. 1,158 m, *Watt 82* (P), *102* (P), *Skutch 145* (US); Mabess River, below Vinegar Hill, 915 m, *Underwood 1315* (NY); trail from Morces Gap to Vinegar Hill, 1,175-1,500 m, *Maxon & Killip 716* (F, GH, NY, US); Seamen's Valley, 150-250 m, *Maxon & Killip 7* (F, GH, NY, US); Dollwood, 915 m, *Harris 7277* (NY), *Jenman s.n.* (NY); Hardwar Gap, 1,219 m, *Crosby et al. 521* (DUKE, GH, MICH); spur of John Crow Mts. opposite Mill Bank, 450-625 m, *Maxon 9307* (NY, US). ST. ANNE: Blue Mts., Trafalgar, *Perkins 1161* (G, GH). ST. THOMAS: Mansfield and adjoining properties, near Bath, 300-500 m, *Maxon 2388* (NY, US); Mansfield near Bath, 1861, *Gilbert s.n.* (BM, GH); Corn Puss Gap and vicinity, trail W over Blue Mts., 610 m, *Wilson & Murray 563* (GH, MICH); Cuna Cuna trail, above Mattis River,

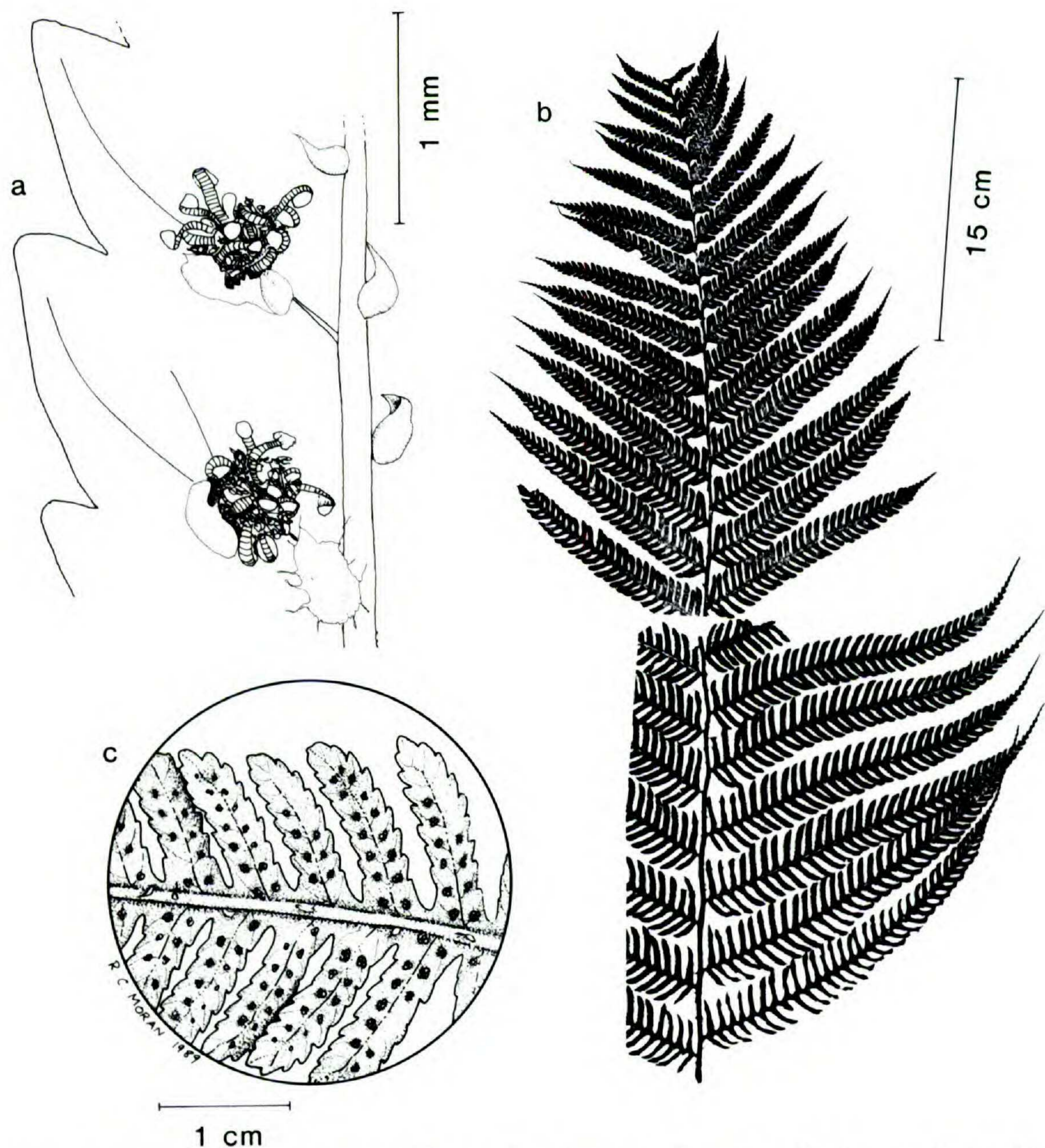


FIGURE 18. *Stigmatopteris jamaicensis* (Maxon 1738, US).—a. Sori subtended by an indusiumlike scale, and bullate and ovate scales on the costule.—b. Distal two-thirds of the lamina.—c. Abaxial surface of a pinna.

300–500 m, *Maxon & Killip 169* (F, GH, NY, US); Bath to Cuna Cuna Pass, *Chrysler 4777* (MICH); near Cuna Cuna Pass, 823 m, *Underwood 2696* (NY); mountain trail between House Hill and Cuna Cuna Gap, 550–725 m, *Maxon 8898* (GH, NY, US), *8963* (NY, US); Cuna Cuna Gap and vicinity, 600–725 m, *Maxon 9158* (GH, US). PARISH UNKNOWN: without locality, *Jenman 60* (UC), *62* (UC), *77* (UC); *Hart 200* (US); *Sherring s.n.* (US); slopes above Tweedside, 610–915 m, *Maxon 970* (US); lower slopes of Mt. Moses, 610 m, *Maxon 1071* (US); Blue Mts., *Linden 1683* (P).

Stigmatopteris jamaicensis is endemic to Jamaica where it grows in wet forests, 150–1,200(–1,500) m. It can be distinguished from all other species of *Stigmatopteris* by the bullate scales on the costules. Walker (1966) counted the chromosomes of this species and found that $n = 41$. This is the only count known for the genus.

12. *Stigmatopteris killipiana* Lellinger, Proc. Biol. Soc. Wash. 89: 730, fig. 8. 1977. TYPE:

Colombia. Chocó: hillside above Río Mutata ca. 3 km above its junction with the Río El Valle, near Alto del Buey, ca. 850 m, *Lellinger & de la Sota 194* (holotype, US; isotypes, COL, CR, HUA not seen, LP not seen; photos DUKE, F, G, GH, MO, NY, UC ex US). Figure 19. Map 4.

Rhizome erect or short-creeping; leaves 70–150 cm; petiole ca. equaling the lamina, abaxially atropurpureous and lustrous, adaxially stramineous or tan, scaly and with a scurf, the scales of two types, the first type 2–5 mm, opaque, appressed, shiny black abaxially, entire, ovate-lanceolate, slightly falcate, the second type 4–9 mm, translucent, spreading, brownish, lanceolate, the scurf appressed, arachnoid, cauducous, light brown or tan; lamina 1-pinnate, oblong-deltate to lanceolate, buds lacking, free pinna pairs 5–13; medial pinnae 14–18(–26) × 3–4.5 cm, widest at or just above the

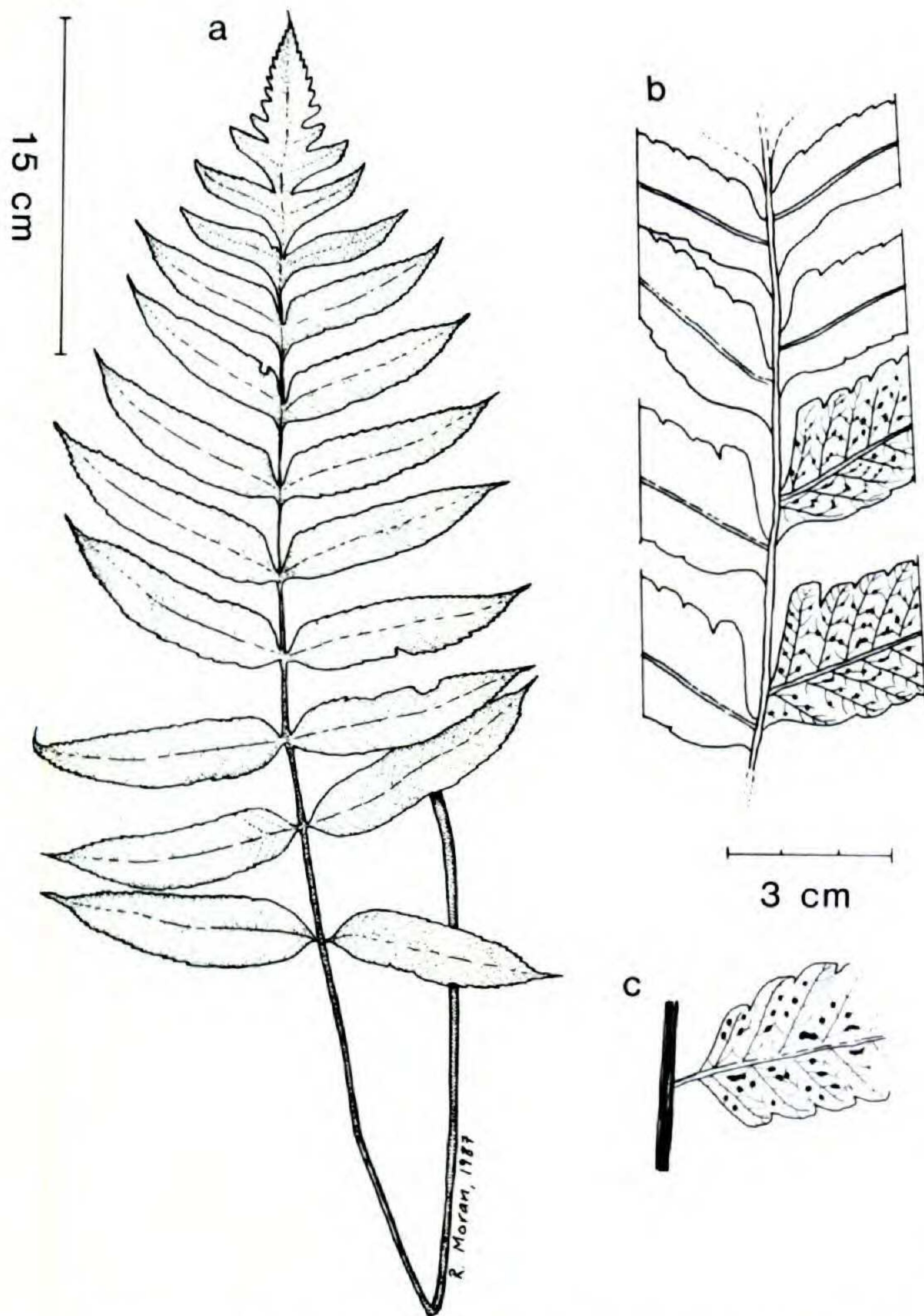
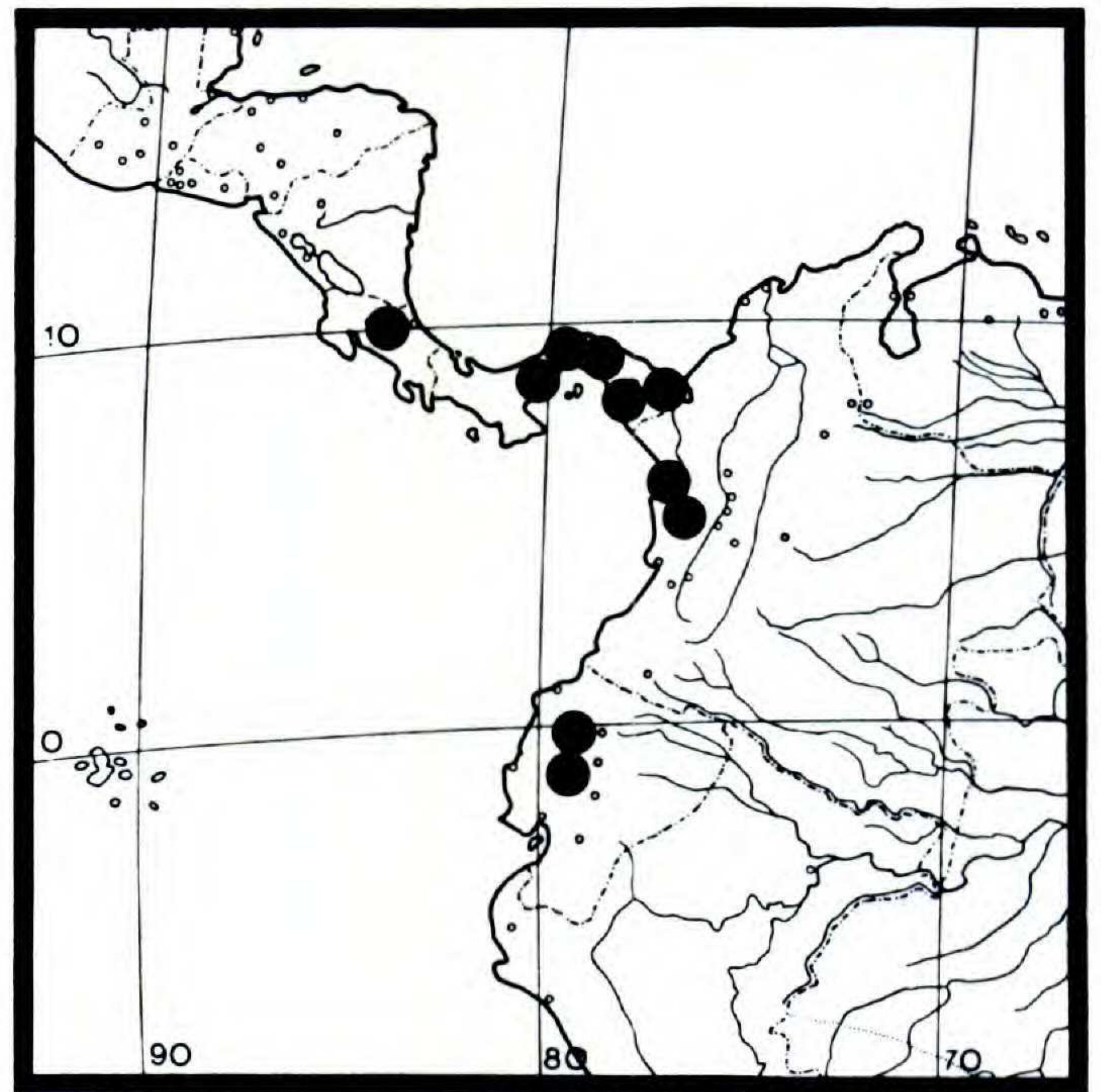


FIGURE 19. *Stigmatopteris killipiana*.—a. Leaf (Moran 3611, MO).—b. Distal part of the lamina showing the transition from decurrent to nondecurrent pinna bases (Grayum et al. 5495, MO).—c. Basal portion of a basal pinna (Grayum et al. 5495, MO).

base, the margins entire to crenate, the base sessile, the upper pinnae with a short decurrent base; basal pinnae ca. equaling the above pinnae, widest at or just below the middle, stalked, the stalk 2–3 mm; rachis atropurpureous at the base, the costae stramineous, both axes lacking hairs, scaly, the scales lanceolate to linear, not fibrillose, scattered; veins partly free and partly anastomosing irregularly; sori discrete or confluent with adjacent one where the veins anastomose, an indusial scale lacking.

Additional specimens examined. COSTA RICA. SAN JOSÉ: hills at SW part of Montañas Jamaica, ca. 2.5 km NE of Bijagual de Turrubares, Carara Reserve, 460–520 m, Grayum et al. 5495 (MO). PANAMA. CANAL ZONE: Pipeline road from Gamboa, Armond 557 (DUKE); NW of Gamboa along "Pipeline Road," McAlpin 1396 (DUKE); near Frijoles, Killip 2919 (US); between Frijoles and Monte Lirio, 30 m, Killip 12147 (GH, US). COCLÉ: El Valle de Anton, 800 m, Alston 8803 (BM, MO), 700 m, Alston 8848 (AAU, BM, CR, F, UC, US); Parque Nacional Soberanía, camino del Oleoducto, Río Pilón, Vásquez 209 (UC), 245 (UC). DARIÉN: Cerro Sapo, ca. 5 km S of Garachiné, along ridge at north approach to cerro, in mixed forest just above *Phytelephas* slope, 600–800 m, Hammel et al. 14827 (MO); middle slopes on the W side of Cerro Pirre, 550–760 m, Croat 68882



MAP 4. Distribution of *Stigmatopteris killipiana*.

(MO). PANAMÁ: along road to Alto de Pacora, 2 km N of turnoff to Cerro Jefe radio tower, Hammel 4858 (CR, MO). COLOMBIA. CHOCÓ: Municipio de Nóvita, vereda Curundó, margen izquierda del Río Ingará, 720 m, Franco et al. 1148 (COL). ECUADOR. LOS RÍOS: Río Palenque Biological Station, km 56 N of Quevedo, 150–220 m, Moran 3611 (MO, QCA), Evoy 44 (NY), Grayum & Zamora 9375 (MO, UC). PICHINCHA: Hotel Tinalandia, ca. 25 km E of Santo Domingo de Los Colorados, N side of Río Toachi, 1,000 m, Moran 3562 (MO, QCA).

Stigmatopteris killipiana grows in and along streambeds from Costa Rica to Ecuador (Map 4), from 30 to 1,000 m. It differs from the similar species *S. pterorhachis* and *S. heterophlebia* by its atropurpureous rachis with abundant scurf and by the greater number of free pinna pairs (5–13) beneath the pinnatifid apex. It further differs from *S. heterophlebia* by its nonpuberulent axes.

13. *Stigmatopteris lechleri* (Mett.) C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. ser. 8, 6: 28. 1920. *Phegopteris lechleri* Mett., Fil. Lechler. 2: 25. 1859. TYPE: Peru. Puno: San Gabán, Lechler 2497 (holotype, B; fragments, BM). Figure 20. Map 5.

Polypodium cyclocolpon Bommer & Christ, Bull. Herb. Boissier sér. 2, 4: 659. 1896 [Bull. Soc. Roy. Bot. Belgique 35: 216. 1896]. *Dryopteris cyclocolpa* (Bommer & Christ) C. Chr., Index Filic. 260. 1905. *Stigmatopteris cyclocolpa* (Bommer & Christ) C. Chr., Amer. Fern J. 4: 82. 1914. TYPE: Costa Rica. Limón: Forêts de Tsâki, Talamanca, 200 m, Apr. 1885, Tonduz 9480 (holotype, BR not seen; isotypes, US, fragment B, photo BM ex BR).

Stigmatopteris ecuadorensis C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. ser. 8, 6:

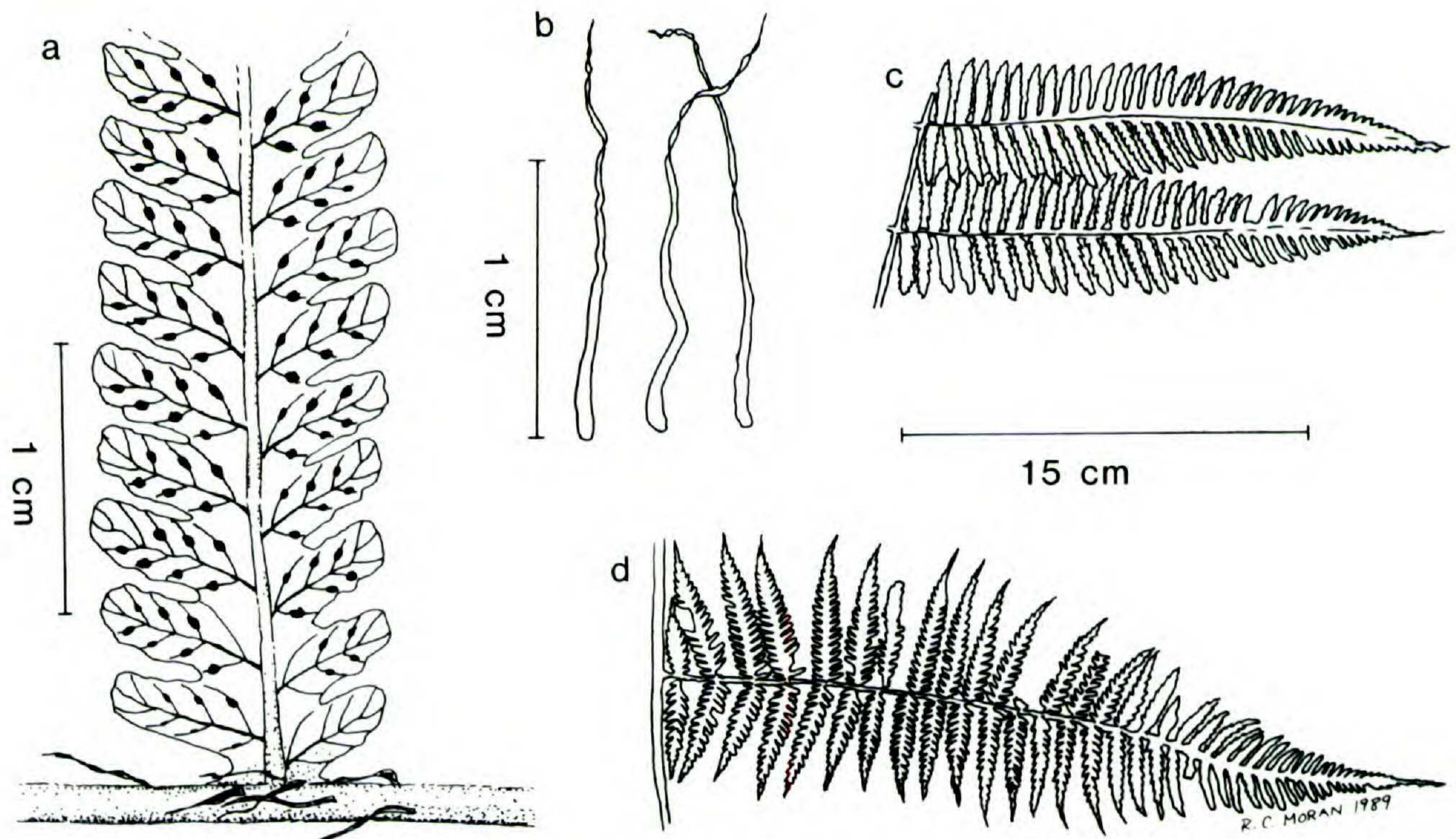


FIGURE 20. *Stigmatopteris lechleri* (Moran 3582, MO).—a. Basal part of pinnule.—b. Petiole scales.—c. Medial pinnae.—d. Basal pinna.

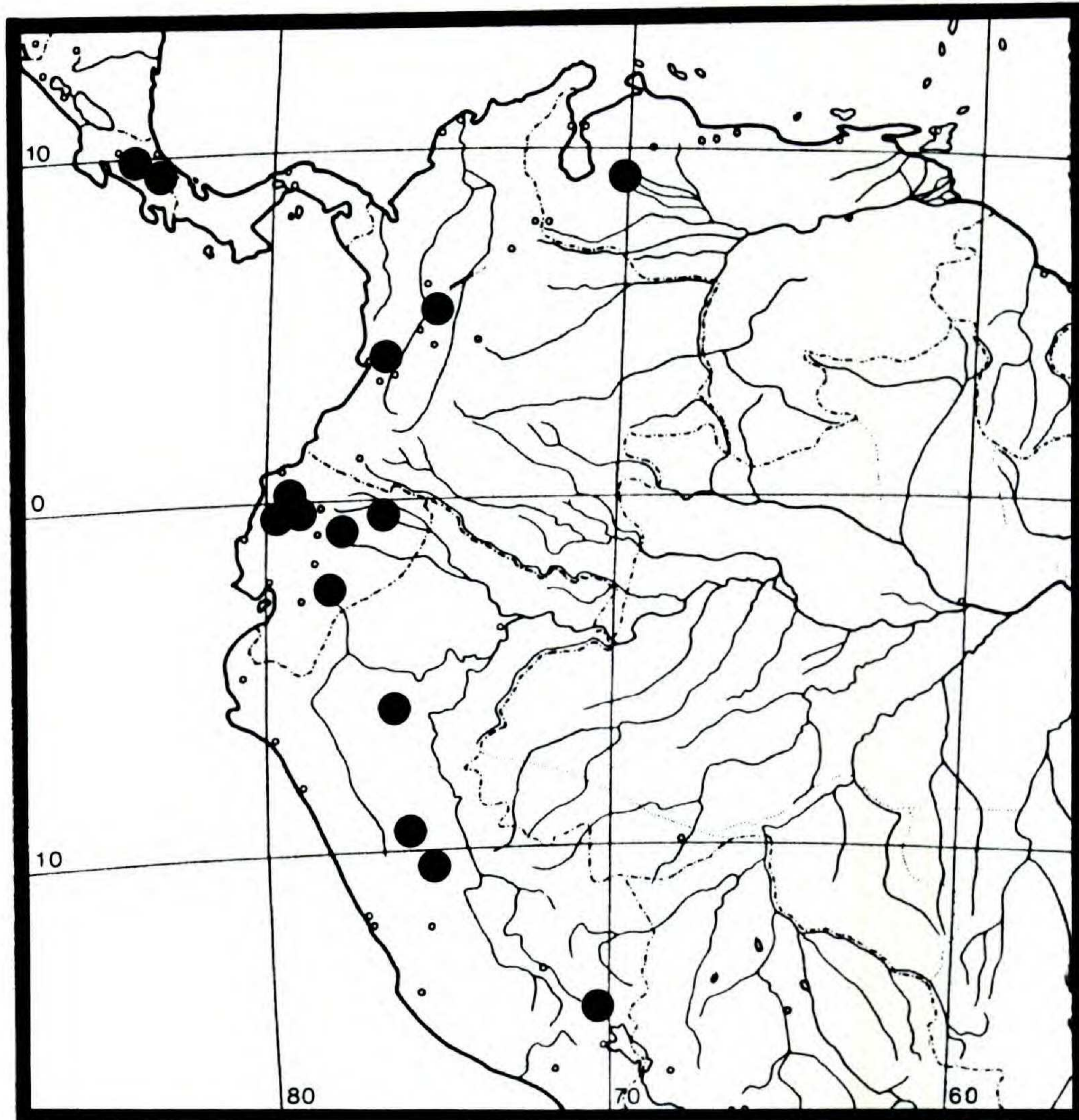
29. 1920. TYPE: Ecuador. "Andes of Quito," *Sodirop* s.n. (holotype, B; isotypes, BM, P in herb. Christ). *Polypodium punctatum* Spruce in Hook., Sp. Fil. 4: 262. 1862, nom. illeg., non (L.) SW. 1802. *Polypodium prasinum* Baker, Syn. Fil. 312. 1867, nom. nov. for *P. punctatum* Hook., with the same type. *Dryopteris prasina* (Baker) C. Chr., Index Filic. 285. 1905. *Stigmatopteris prasina* (Baker) C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. ser. 7, 10: 79. 1913. LECTOTYPE (designated by Christensen, 1913): Peru. San Martín: Tarapoto, Mt. Guayrapurima, Aug. 1856, *Spruce* 4719 (K; isoelectotypes, BM, G, P; photos F, MO ex K).

Rhizome erect-ascending; petioles ca. equaling the lamina, brown to tan, scaly, especially toward the base, the scales $8\text{--}20 \times 1\text{--}2\text{--}(3)$ mm, lanceolate to linear, brown to blackish, the margins flat or enrolled, entire; lamina 2-pinnate-pinnatifid, $0.6\text{--}1.2 \times 0.4\text{--}0.8$ m, deltate or nearly so, bulblets absent; pinnae $25\text{--}40 \times 5\text{--}15$ cm, widest at the base, not overlapping the rachis; pinnules $4\text{--}10 \times 1\text{--}2.3$ cm, narrowly lanceolate-triangular, sessile to broadly adnate and decurrent, lobed to pinnatisect; lobes oblong to rectangular, entire to serrate apically; rachis and costae stramineous or brown, scaly, the scales linear or narrowly triangular, tortuous, fibrillose; veins unbranched or rarely (in the larger segments) branched, nearly reaching the margin; sori lacking an indusial scale.

Additional specimens examined. COSTA RICA. LIMÓN: Cantón de Talamanca, Amubri, margen izquierda del Río Urén, Loma Sheub, 150 m, *Herrera* Ch. 2980 (CR, MO). Zona Protectora Barbilla, W side of plateau separating headwaters of N fork of Río Dantas from headwaters of

Quebrada Barreal, Río Barbilla drainage, 600–660 m, *Grayum et al.* 7922 (MO, UC, US). VENEZUELA. PORTUGUESA: Dto. Sucre, Villa Rosa, 15 km SE de Biscucuy, bosques nublados a lo largo de la quebrada El Potrero, 1,400–1,600 m, *Aymard et al.* 3747 (NY, PORT, UC). COLOMBIA. CALDAS: Santa Cecilia, Cordillera Occidental, vertiente Occidental, 800 m, *von Sneidern* 5046 (F, US). EL VALLE: Digua Valley, Río Blanco, 500 m, *Alston* 7842 (BM). ECUADOR. MORONA-SANTIAGO: Cordillera de Cutucú, western slopes, along trail from Logroño to Yaupi, 1,600 m, *Madison et al.* 3472 (GH, QCA). NAPO: 15 km N of Tena along road to Baeza, 1,100 m, *Moran* 3582 (MO, QCA, QCNE); Cantón Archidona, faldas S del Volcán Sumaco, carretera Hollín-Loreto, km 31, comuna challa Yacu, 1,200 m, *Palacios* 4030 (MO, QCNE); *Moran* 5119, MO, QCNE; Francisco de Orellana, cerca del Cañón de los Monos en Potrero, 250 m, *Zak & Jaramillo* 3635 (MO). PICHINCHA: carretera Quito-Puerto Quito, km 113, 10 km N de la carretera principal, Reserva de ENDESA, Corporación Forestal Juan Manuel Durini, 800 m, *Moya* 0011 (AAU); freq. in silvis de los Colorados, Oct. 1883, *Sodirop* s.n. (SI, UC); crescit in silvis tropicis ad San Miguel, Aug. 1875, *Sodirop* s.n. (fragment, B). PERU. HUÁNUCO: 25 km NE of Tingo María, La Divisoria, 1,700 m, *Moran* 3696 (MO, USM). PASCO: Provincia Oxapampa, Gran Pajonal, 2–3 km N of Chequitavo, 1,200 m, *D. N. Smith* 5082 (MO).

Stigmatopteris lechleri occurs from Costa Rica to Venezuela and Peru (Map 5), from 200 to 1,700 m. It is easily identified by its 2-pinnate-pinnatifid lamina, which is the most finely divided in the genus. The petiole scales vary considerably. Specimens from most parts of the range have linear or narrowly triangular scales with inrolled margins, but specimens from Colombia have wider lanceolate scales with flat (not inrolled) margins. Since intermediate specimens exist and no other character



MAP 5. Distribution of *Stigmatopteris lechleri*.

correlates with the scale differences, the variation does not merit nomenclatural distinction.

Christensen (1920) distinguished *S. cyclocolpa* and *S. ecuadorensis* from *S. lechleri* by the degree of pinnule adnation and cutting. However, these characters are variable, even on a single leaf as one goes from the more highly divided base to the less-divided medial regions. Apparently, Christensen saw only incomplete type material, which represented the different degrees of cutting.

14. *Stigmatopteris longicaudata* (Liebm.) C. Chr., Bot. Tidsskr. 29: 300. 1909. *Polypodium longicaudatum* Liebm., Kongel. Vidensk. Selsk. Skr., Naturvidensk. Afd. ser. 5, 1: 209. 1849. *Dryopteris longicaudata* (Liebm.) Maxon, Contr. U.S. Natl. Herb. 13: 18. 1909. SYNTYPES: Mexico. Veracruz: "Baranca de Huitamalco," Liebm. s.n. [Liebm. Pl. Mex. 2694, Flora Mex. 737, 738, 739] (lectotype, 737, chosen by A. R. Smith, Fl. Chiapas, Part 2, 213. 1981: C—folio herbarium not seen; isolectotype, K). Figure 21. Map 6.

Stigmatopteris palmensis Rosenstock, Repert. Spec. Nov. Regni Veg. 22: 12. 1925. TYPE: Costa Rica. San José: La Palma, Brade & Brade 497 (holotype, S? not seen; isotypes, UC, US).

Rhizome erect or creeping, the internodes ca. 1 cm, the scales 1–2 mm, black, rigid, entire, ovate-lanceolate; leaves 0.8–1.4 m; petiole $\frac{1}{2}$ to equaling the lamina, brown or less often stramineous, the scales of two types, the first type 2–5 mm, opaque, appressed, shiny black, entire, ovate-lanceolate, the second type 4–9 mm, translucent, spreading, brownish, lanceolate; lamina 1-pinnate, ovate to subdeltate, lacking bulbils; pinnae mostly 14–20 \times 2–2.5 cm, linear to narrowly lanceolate, 12–20 pairs, entire, crenate, or cut less than $\frac{1}{4}$ ($-\frac{1}{3}$) to the costae; pinnae confluent in the distal $\frac{1}{2}$ – $\frac{1}{3}$ of the lamina by the decurrent pinna bases, lower pinnae free, sessile, or stalked, the stalk 2–5 mm; rachis and costae glabrous to densely scaly, the scales ovate to lanceolate, or (in Venezuela, Peru, and Bolivia) linear and fibrillose; veins free, or with a few casual anastomoses, 3–6 per segment; sori lacking an indusiumlike scale, medial to suprasedial, filiform scales present among the

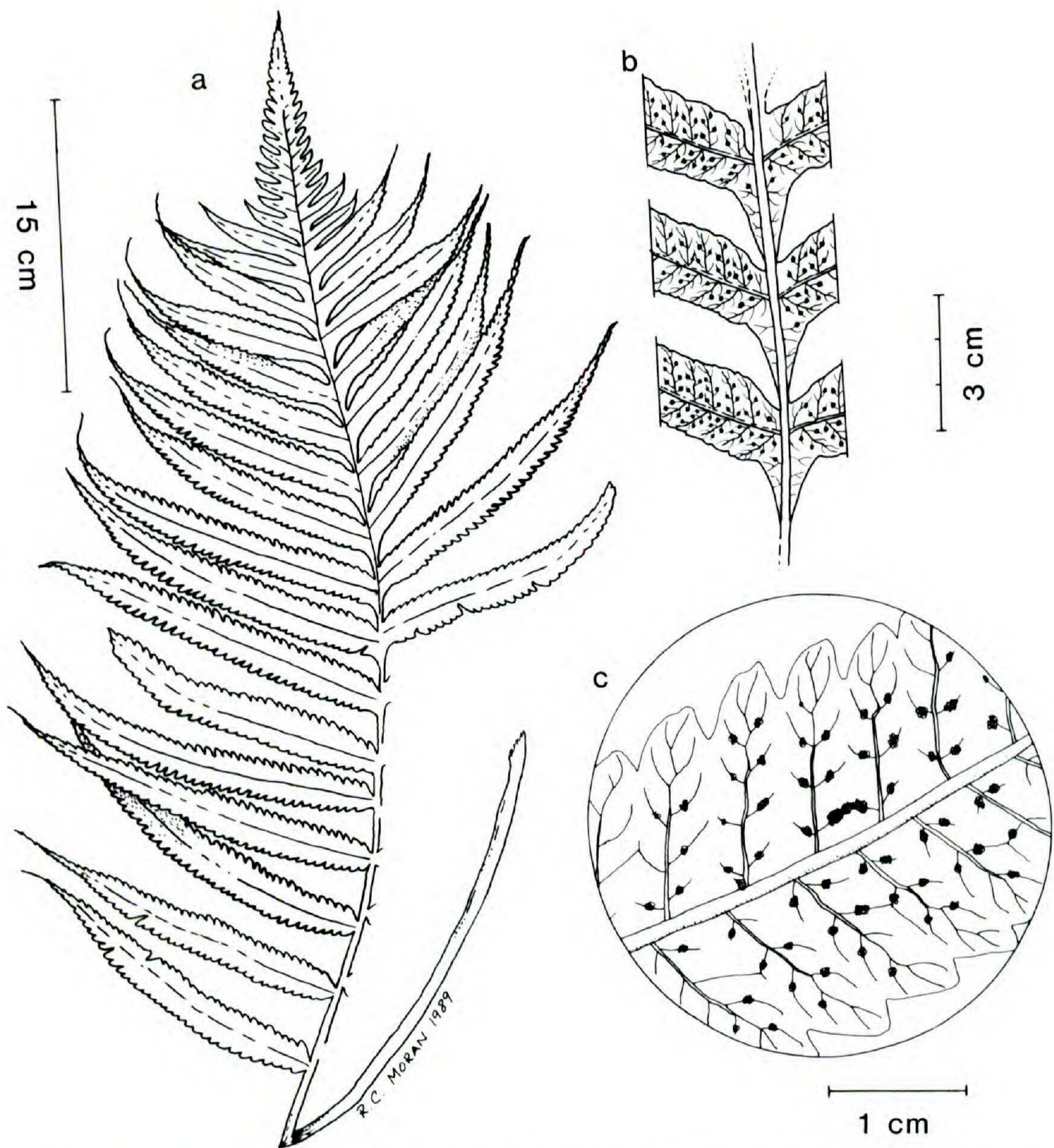
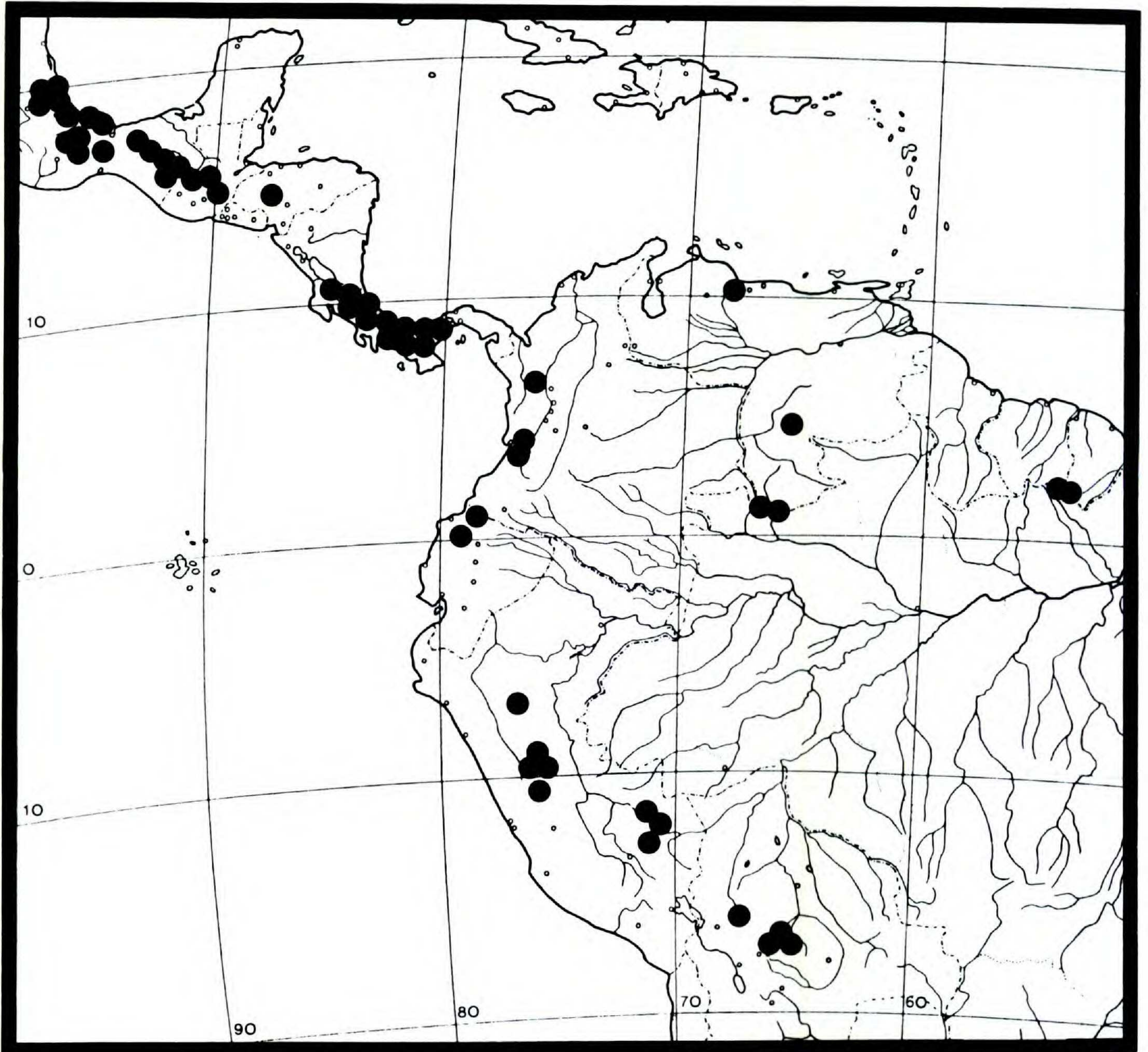


FIGURE 21. *Stigmatopteris longicaudata*. —a. Leaf (Moran 3206, MO). —b. Medial pinnae showing decurrent bases (Liesner & Stannard 16909, NY). —c. Venation and sori (Moran 3206, MO).

sporangia in plants from Venezuela, Peru, and Bolivia.

Additional specimens examined. MEXICO. CHIAPAS: 10 km above Rayón Mezcalapa along road to Jitotol, Municipio of Rayón, 1,700 m, *Breedlove & Smith 32672* (F, MICH, NY); Monte Bello National Park, Municipio of La Trinitaria, 1,300 m, *Breedlove 35128* (F, MO); E of Laguna Tzikaw, Monte Bello National Park, Municipio of La Trinitaria, 1,300 m, *Breedlove 35028* (MICH, MO, NY); 10 km ENE of Dos Lagos above Santa Elena, Municipio of La Trinitaria, 1,170 m, *Breedlove 56494* (MICH, MO, NY); near Ixtacomitan, 490 m, *Rovirosa 822* (K, PH). OAXACA: Dto. Villa Alta, valley of the Yelagago River, ca. 20 mi. NE of Villa Alta, *Mickel 975* (MICH, US), 2,072 m, *990* (MICH, US); Dto. Ixtlán, 79 km N of Ixtlán de Juárez on Rte. 175, 1 km S of Campamento Vista Hermosa, 1,100–1,200 m, *Mickel 5662* (NY, UC, US); Dto. Ixtlán, 29 km S of Valle Nacional, 80 km N of Ixtlán de Juárez, ca. 500–600 m, *Mickel 6369* (NY); 29 km S of Valle Nacional, 80 km N of Ixtlán de Juárez, *Mickel 6392* (NY); Dto. Ixtlán, 7 km S of Vista Hermosa, 71 km N of Ixtlán de Juárez on Rte. 175, 1,645 m, *Mickel & Pardue 6727* (NY);

Dto. Ixtlán, 2–3 km S of Vista Hermosa, 75–76 km N of Ixtlán de Juárez on Rte. 175, 1,615 m, *Mickel & Pardue 6543* (NY, UC); road from Oaxaca to Tuxtepec, km 125–153, *Hellwig 491* (NY), *492* (NY), *494* (NY); Ixtlán–Tuxtepec road, 35–39 km S of Valle Nacional, km 96–100, *Mickel 1523* (MICH, NY, US); hwy. through Sierra de Juárez between Tuxtepec and Oaxaca, 21.5 mi. S of bridge at Valle Nacional, S of La Esperanza, 1,660 m, *Croat 48097* (CR, MO); 47 mi. from Ixtlán on Rte. 175, *McAlpin 1043* (DUKE); Dto. Tehuantepec, along Continental Divide between La Chiguzhe and Guevea de Humboldt, ca. 1,200 m, *Hallberg 1724* (NY). PUEBLA: Limonateno, Municipio de Hueytamalco, 1,000 m, *Mickel 484* (MICH), *Ventura A. 484* (NY). VERACRUZ: 6 km by road N of Paz de Enríquez, Municipio Yecuatla, 1,200 m, *Nee et al. 26382* (F, NY, Z); Plan de Almansa, Municipio de Yecuatla, 600 m, *Ventura A. 3306* (CR, NY); Lomas de Santa Rita, Municipio de Yecuatla, *Ventura A. 3630* (NY); camino Bastonal a Santa Marta, Municipio Catemaco, *Gómez-Pompa et al. 5457* (F); La Calavera, 5 km adelante de Atalen, Municipio de Atzalan, *Calzada 5212* (F); 9 km E of Tebanca (9 km E of Lago Catemaco), 980 m, *Nee & Schatz 19868* (F); 12 km S of Misantla, 1,350 m, *Bohs et al. 1704* (GH); ca. 8 km



MAP 6. Distribution of *Stigmatopteris longicaudata*, the most widely distributed species in the genus.

S of Misantla, ca. 750 m, *Conant* 792 (GH), *Barrington* 410 (GH); Santa Rita prope Misantla, *Hahn* 352 (MO, P); Cordova, *Finch* 169 (UC). GUATEMALA. ALTA VERAPAZ: Hochwald bei Purulhá, 1,800 m, *von Türckheim* 111691 (GH, NY, P, US). BAJA VERAPAZ: Salama, Aldea San Rafael Chilasco, *Guzmán-Valdez* 892 (F); Hochwald in Pauyal, 1,350 m, *von Türckheim* 3865 (GH, US). HUEHUETENANGO: vic. of Maxbal, 17 mi. N of Barillas, 1,500 m, *Steyermark* 48744 (F, US); Cerro Negro, 2 mi. E of Las Palmas, 1,600–2,000 m, *Steyermark* 51710 (F, US). HONDURAS. COMAYAGUA: hills above Varsovia, near town of Cerro Azul, 900 m, *Hazlett* 3029 (MO). COSTA RICA. ALAJUELA: ca. 20 km N of San Ramón, at the Univ. of San Ramón's Biological Field Station, cloud forest, 1,100 m, *Moran* 3206 (CR, F, GH, MO); Monteverde Cloud Forest Reserve, 1,520–1,580 m, *Dryer* 366 (F); Monte Verde Reserve, Atlantic slope in valley or Río Peñas Blancas, 900–950 m, *Hammel et al.* 14238 (MO). CARTAGO: ca. 10 km SE of Tapantí, *Wilbur & Stone* 8919 (DUKE); 16 km S of Tapantí, *Stolze* 1487 (CR, F, UC); Tapantí, 1,300–1,800 m, *Gómez* 18778 (CR, MO, PORT, UC); Tapantí, Quebrada Valverde, *Gómez & Wagner* 6856 (CR); Tapantí Hydroelectric Reserve, 1,500 m,

Croat 36176 (CR, MO); along tributary of Quebrada Casa Blanca Tapantí, 1,350 m, *Grayum & Sleeper* 3683 (MO, UC); trail leading E into mountains from road into Tapantí Reserve, ca. 1 km S of jct. of Quebrada Salto and Río Grande de Orosi, 1,500–1,800 m, *A. R. Smith et al.* 2194 (CR, MO, UC); ca. 15 km S of Tapantí along the new road, on the E slope above the Río Grande de Orosi near the concrete bridge, 1,500 m, *Burger & Liesner* 6773 (CR, F, GH). HEREDIA: Estación Biológica La Selva, at confluence of Río Sarapiquí and Río Puerto Viejo, Atlantic slope, 50–80 m, *Grayum et al.* 7910 (DUKE, MO); vic. of La Palma, on the road to La Hondura, 1,500–1,700 m, *Maxon & Harvey* 8075 (US); Sardinal, 1,600 m, *Gómez* 2182 (CR, F, GH, NY, UC, US); area between Río Peje and Río Ardinalito, Atlantic slope of Volcán Barva, 480–520 m, *Grayum* 6893 (MO); Zona Protectora, N slopes of Volcán Barva, between Río Peje and Río Guacimo, along Quebrada Cantarana, 190 m, *Grayum & Schatz* 3089 (DUKE); Zona Protectora-Q, Canta Rana Magsasay, 400 m, *Chacón* 852 (CR). SAN JOSÉ: along unnamed N fork of Río Zurqui, 1,500–1,600 m, *A. R. Smith et al.* 1678 (MO, NY, UC). PANAMA. BOCAS DEL TORO: vic. of Cerro Colorado, on trail along creek

8.6 mi. from Camp Chami, 1,400 m, *McPherson 8885* (MO, UC); Cerro Colorado, ca. 8.6 mi. W of Chamé, *Croat 69108* (MO, NY, PMA, UC, US); along road between Fortuna Dam and Chiriquí Grande, 8.5 km N of bridge, 4.3 km N of Continental Divide, *Croat & Grayum 60177* (MO, UC); along road between Fortuna Dam and Chiriquí Grande, 7.3 mi. N of bridge, 3.2 mi. N of Continental Divide, 700 m, *Croat & Grayum 60215* (MO). CHIRIQUÍ: vic. of Cerro Colorado mine above San Felix, 1,450 m, *McPherson 12035* (MO); above Boquete, on trail to Pate Macho on Continental Divide, 1,850–2,100 m, *McPherson 12310E* (MO); Canassa, 2,500 m, *Killip 5444* (US). COCLÉ: El Valle, *González 14* (MO); La Mesa, above El Valle de Antón, ca. 2 km W of Cerro Pilon, 900 m, *Croat 37492* (MO, US); upper Caldera watershed, between "Camp I" and the divide, Holcomb's trail, above El Boquete, 1,650–1,925 m, *Maxon 5647* (NY, US); Holcomb's Trail, above El Boquete, 1,675–1,800 m, *Killip 5344* (GH, US). VERAGUAS: Cerro Tute, ca. 2 km N of Santa Fé, 900–1,100 m, *Moran 4048* (MO, STRI, UC); along Río Dos Bocas, ca. 12 km beyond Santa Fé, 450 m, *Croat 25818*, (MO), 27736 (MO); 11 km from Escuela Agrícola Alto Piedra on road to Calovebora, 450 m, *Croat 27541* (MO); 5 mi. W of Escuela Agrícola Alto Piedra, 800–1,200 m, *Croat 22998* (MO, NY); area of Santa Fé, road past Escuela Agrícola Alto Piedra, 700 m, *Churchill et al. 5984* (MO, UC). FRENCH GUIANA. Tumuc Humac, à mi-chemin entre le Mitaraka Sud et le Toukouchipann, 480 m, *de Granville 1291* (Z); Tumuc Humac, au SE du Mitaraka Sud, 400 m, *de Granville 1434* (NY, P, Z). VENEZUELA. CARABOBO: las laderas arriba de las cabeceras de Río San Gián, E de Los Tanques, S de Borburata, 750–1,100 m, *Steyermark & Steyermark 95406* (GH, VEN). TERRITORIO DE AMAZONAS: Depto. Atures, lower forested E slope of 1,760 m peak, 8 km NW of settlement of Yutuje, 3 km W of Río Coro-Coro, W of Serranía de Yutaje, 1,050–1,200 m, *Liesner & Holst 21882* (MO, UC); Depto. Río Negro, Cerro de Neblina Camp V., valley north base of Pico Cardona, 1,250 m, *Liesner & Stannard 16909* (F, MO, NY, UC, US); Cerro de Neblina, Río Yatua, 5–8 km S of Camp 3, 1,100–1,600 m, *Maguire et al. 36864* (F, MICH, NY). COLOMBIA. ANTIOQUIA: Municipio de Frontino, road between Nutibara and La Blanquita, region of lower Murri, ca. 28 km from Nutibara, 960 m, *MacDougal et al. 3811* (MO, UC). EL VALLE: Cordillera Occidental, vertiente occidental, Hoya del Río Digua, lado derecho, La Elsa, quebrada La Cristalina, 1,000–1,150 m, *Cuatrecasas 15240* (F, US); Cordillera Occidental, vertiente occidental, Hoya del Río Digua, lado izquierdo, Piedra de Moler, 900–1,180 m, *Cuatrecasas 15122* (F, US). ECUADOR. PICHINCHA: NE of Vicente Maldonado, Reserva de ENDESA, 600 m, *Laegaard 52431* (AAU, MO). CARCHI: wet plateau above San Marcos de los Coaiques, trail toward Gualpí Bajo, 1,000 m, *Øllgaard et al. 57515* (AAU, MO). PERU. CUZCO: Province Paucartambo, Cosñipata Valley, Río Tono, first foothill ridge on road N of Patria, 800 m, *Wachter et al. 200* (F). HUÁNUCO: Tingo María, 700 m, *Tryon & Tryon 5330* (BM, F, GH). JUNÍN: E of Quimirí Bridge, near La Merced, 800–1,300 m, *Killip & Smith 23906* (NY, US); ridge E of Tingo María, 625–1,100 m, *Allard 22558* (US). MADRE DE DIOS: Province Manú, Cerro de Pantiacolla, Río Paltoa, 10–15 km NNW of Shintuya, transect to ridge top, 700–1,000 m, *Foster et al. 10908* (F); Parque Nacional del Manú, Cocha Cashu Biological Station, *Foster P-84-91* (F). SAN MARTÍN: Mt. Guayrapurima, near Tarapoto, *Spruce*

4012 (BM, G, K, P). UCAYALI: Province Coronel Portillo, Sinchono, cerca de la Divisoria, 1,500 m, *Aguilar 861* (GH, USM); Sinchono, entre Tingo María y Pucallpa, 1,500 m, *Aguilar 865* (GH). BOLIVIA. COCHABAMBA: Province Carrasco, Antahuacana, Quebrada Espíritu Santo, 750 m, *Buchtien 64* (P), 2166 (BM); Province Carrasco, confluencia del Río Leche con el Río Isarsama, 220 m, *Beck 1625* (UC). LA PAZ: región de Mapiri, San Carlos, 850 m, *Buchtien 233* (GH, MO, UC, US); San José de Mapiri, 750 m, *Cardénas 1020* (GH); Province Nor Yungas, 13 km NE del camino entre Yolosa y Caranavi, por el camino a Suapi, al lado del Río Khusillani, ca. 1 km antes la comunidad Khusillani, 1,500 m, *Solomon 18469* (MO).

Stigmatopteris longicaudata occurs from Mexico to French Guiana and Bolivia (Map 6), 220–2,100(–2,500) m, and is the most widely distributed species in the genus. Its most distinctive features are the pinnae, which are less lobed than most other species and, at least in the distal part of the lamina, have long-decurrent bases (Fig. 21b). The specimens from Peru and Bolivia differ from the rest by the linear and fibrillose scales (vs. ovate-lanceolate) on their axes and veins. No other difference correlates with scale type.

15. *Stigmatopteris michaelis* (Baker) C. Chr., Bot. Tidssk. 29: 300. 1909. *Polypodium michaelis* Baker, J. Bot. 6: 164. 1877. TYPE: Ecuador. Pichincha: near Santo Domingo de los Colorados, *Sodirol 2615* (holotype, K; isotypes, P, Q, SI). Figure 22. Map 7.

Polypodium sylvicola Baker, J. Bot. 19: 205. 1881. *Dryopteris sylvicola* (Baker) C. Chr., Index Filic. 297. 1905. TYPE: Colombia. Antioquia: 1,000 m, *Kalbreyer 1807* (holotype, K).

Rhizome short-creeping; leaves 30–70 cm; petioles $\frac{2}{3}$ to equaling the lamina, the base dull brown, becoming stramineous distally, scaly, the scales opaque, black, appressed, or membranous, tan, and spreading; leaves 0.3–0.7 m long; lamina 1-pinnate-pinnatifid, winged for $\frac{2}{3}$ – $\frac{3}{4}$ the length, narrowly deltate to lanceolate, the apex evenly attenuate; pinnae (4.5–)9–11 \times (1–)1.8–2.2 cm, pairs 17–20, widest at or slightly above the middle, lobed ca. halfway to the costa, the base of the distal pinnae adnate and decurrent, the base of the basal pinnae stalked, the stalk 1–3 mm; rachis and costae stramineous, scaly, the scales scattered; less than 0.4 mm, filiform, the larger ones with several cilia at their base; veins free, unbranched, (3–)4–6(–7) per segment; sori lacking an indusiumlike scale, paraphysate, the paraphyses ca. equaling the sporangia, uniseriate, multicellular, dark brown, spreading, somewhat tortuous.

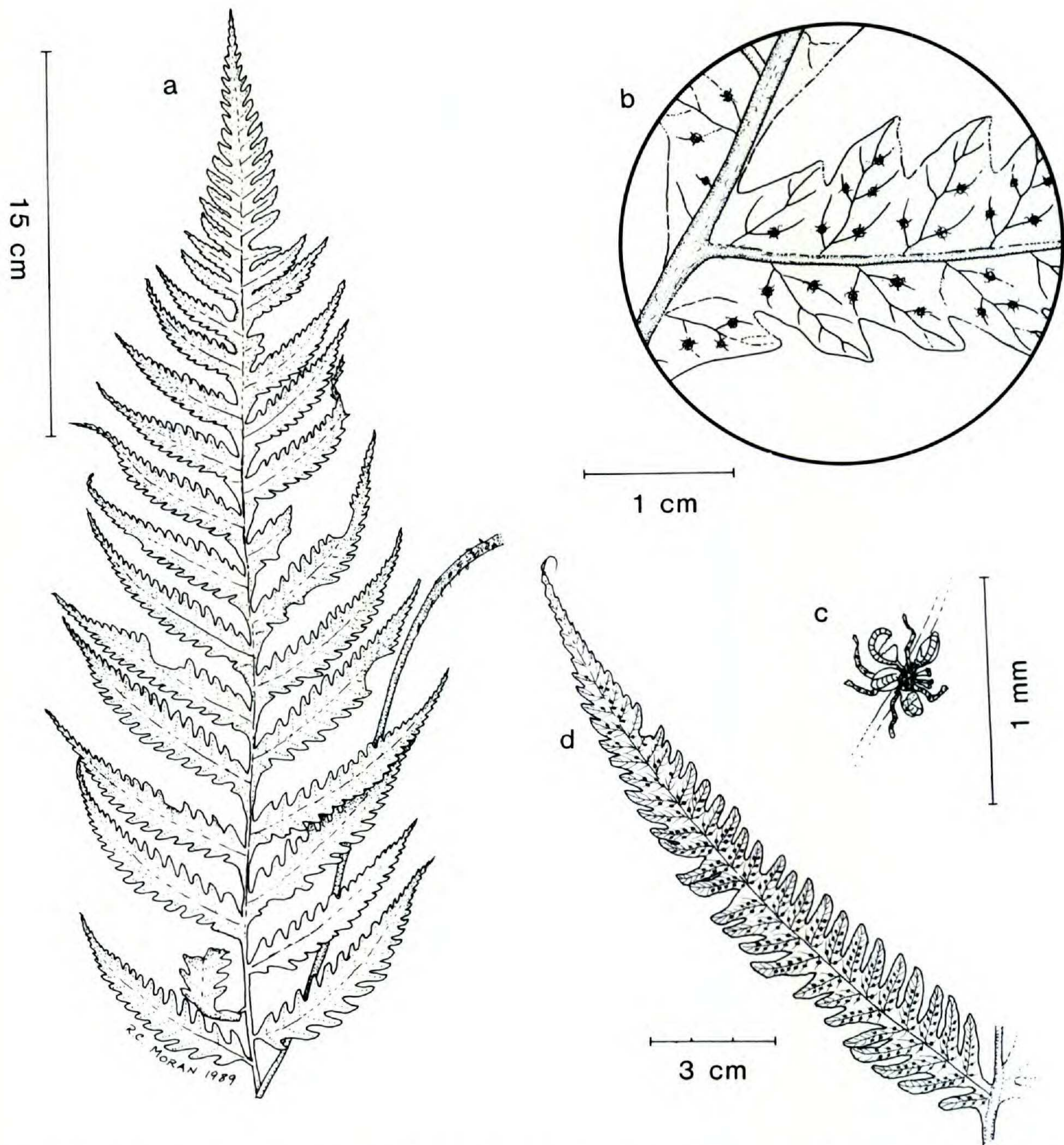


FIGURE 22. *Stigmatopteris michaelis*. —a. Leaf. —b. Base of medial pinnae. —c. Paraphysate sorus. —d. Medial pinna. a, b, *McDonough et al.* 371, MO. c, d, *Sodiro s.n.*, UC.

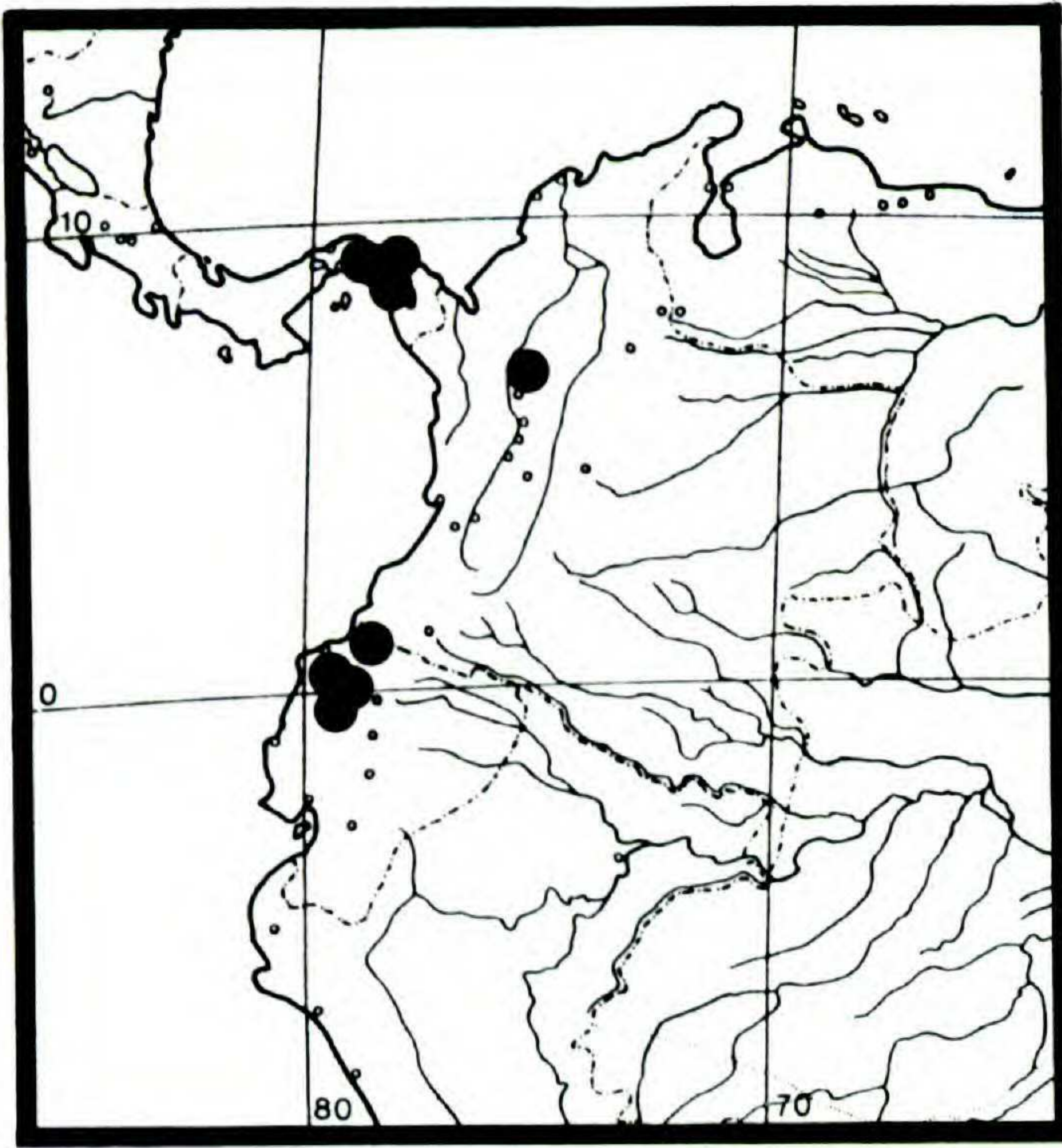
Additional specimens examined. PANAMA. PANAMÁ: Cartí road, ca. 15 km from its beginning, 300 m, *Hammel & Kress* 13398 (DUKE, F, MO, US). COMARCA DE SAN BLAS: trail along continental divide, 400 m, *McDonough et al.* 371 (MO); Nusagandi, El Llano–Cartí road, 350 m, *van der Werff* 7010 (MO, NY, UC). ECUADOR. CARCHI–ESMERALDAS: Lita, 600 m, *van der Werff et al.* 9566 (MO). PICHINCHA: in silvis tropical prope San Miguel, 1882, *Sodiro s.n.* (UC); NE of Vicente Maldonado, Reserva de ENDESA, 600 m, *Laegaard* 52224, (AAU).

Stigmatopteris michaelis occurs from Panama to Ecuador (Map 7) on steep clay banks along streams, from 300 to 1,000 m. It is distinctive by the combination of long-decurrent pinna bases, pinnae lobed about halfway to the costa, and paraphysate sori (Fig. 22). The paraphyses are easily overlooked because they resemble stalks of the

sporangia, but they can be distinguished by their darker color, slightly tortuous habit, and one-celled (not three-celled) apex. In general, *S. michaelis* has a smaller leaf than other species in the genus. The derivation of the specific epithet is unknown.

16. *Stigmatopteris nephrodioides* (Klotzsch) C. Chr., Bot. Tidsskr. 29: 299. 1909. *Polypodium nephrodioides* Klotzsch, Linnaea 20: 384. 1847. TYPE: Venezuela, *Karsten* 9, *Coll. II* (holotype, B). Figure 23. Map 8.

Rhizome short, ascending; leaves to 2 m; petioles ca. ½ to equaling the lamina, tan to brown, the scales 3–13 × 1–2 mm, lanceolate, entire; lamina 1-pinnate-pinnatifid, lanceolate, bulblets lacking;



MAP 7. Distribution of *Stigmatopteris michaelis*.

pinnae 18–25 × 2.1–3.5 cm, cut $\frac{1}{4}$ – $\frac{1}{2}$ to the costa, or rarely more in enlarged basal pinnae, the basal ones stalked, the distal ones gradually becoming sessile, then adnate, the basal basiscopic lobe of the medial pinnae often overlapping the rachis, the basal acroscopic lobe often prolonged; rachis and costae moderately scaly, the scales lanceolate; lobes rounded, entire; veins 4–8 per lobe, unbranched; sori lacking an indusial scale.

Additional specimens examined. VENEZUELA. ANZOÁTEGUI: Cerro Peonía (Cerro Coroy), above Carmelita, between Río León and Bergantín, NE of Bergantín, 1,000–1,450 m, *Steyermark 61403* (F). ARAGUA: along road between Colonia Tovar and Carayaca, 2.3 km below the junction with Colonia Tovar–Caracas road, 750 m, *Croat 54475* (MO, UC); along road between Maracay and Ocumare de la Costa, Henri Pittier National Park, 3 km N of summit, 970 m, *Croat 60576* (NY, UC); near Colonia Tovar, *Fendler 198* (BM, G, GH, K, MO, P, US), *Funck & Schlim 411* (BM, G, P); cloud forests of the valle de Ocumare, 1,100 m, *Pittier 12172* (US, VEN); Parque Nacional Henry Pittier, above Guamitas, along trail to La Mesa, *Steyermark 89747* (GH, US); Cordillera Interior, entre El Pauji y El Socorro, hacia la represa, S de El Consejo, 1,350–1,400 m, *Steyermark & Stoddart 118173-A* (GH, VEN). CARABOBO: ca. 18–20 km S of Puerto Cabello, ca. 9–14 km S of San Esteban on old trail to Valencia, 0–4 km S of colonial bridge, 350–700 m, *Liesner & Medina 13739* (MO, UC, VEN); arriba de las cabeceras del Río San Gián, E de Los Tanques, S de Borburata, *Steyermark & Steyermark 95406-A* (F, GH, NY, US, VEN). DISTRITO FEDERAL: old road between Portachuelo and Peñita (Petaquire and Carayaca), between Colonia Tovar–Junquito road and Hacienda El Limon, 6–8 mi. below junction of Junquito–Colonia Tovar road, *Steyermark & Nevling 95914* (GH, NY, VEN). FALCÓN: Sierra de San Luis, arriba de Sta. María, 1,200 m, *van der Werff 3488* (MO, UC). MIRANDA: Dtto. Paéz,

Fila La Tigra, Quebrada San Juan, 18 km SO de Cúpira, 650 m, *Ortega & González 369* (PORT, MO, UC). YARACUY: along road from Salom to Candelaria, 8–8.5 km above Salom Central Plaza, 1,260–1,290 m, *Croat 60765* (MO, NY, UC); Dtto. Bruzual, Montaña de María Lionza, Quebrada Quibayo, 250–1,000 m, *Steyermark et al. 125086* (UC); Cabeceras de la Quebrada Amparo, El Amparo hacia Candelaria, a 7–8 km N de Salom, 1,220–1,250 m, *Steyermark & Espinoza 111174* (NY, VEN); Dtto. Nirgua, El Amparo, 7–11 km N de Salom, 1,200–1,300 m, *Steyermark & Espinoza 111493* (NY, UC).

Stigmatopteris nephrodioides is endemic to north-central Venezuela (Map 8), where it occurs in wet forests from 650 to 1,450 m. A good character to identify this species is the basal basiscopic lobe of the medial pinnae that overlaps the rachis (Fig. 23a). The only other species of *Stigmatopteris* with pinna bases that overlap the rachis is *S. contracta*, a Costa Rican species that differs greatly in leaf cutting (Fig. 12). The name *S. alloëoptera* (Kunze) C. Chr. may apply to *S. nephrodioides*, but I have not seen the type and therefore cannot be certain (see section on names of uncertain application).

- 17. *Stigmatopteris opaca*** (Baker) C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. ser. 7, 10: 78. 1913. *Meniscium opacum* Baker, J. Bot. 15: 166. 1877. *Phegopteris opaca* (Baker) Christ, Farnkr. Erde 270. 1897, illegit., non (Sprengel) Mett. 1858. *Dryopteris christii* C. Chr., Index Filic. 257. 1905, a nom nov. for *Meniscium opacum* with the same type, non *Dryopteris opaca* (Don) C. Chr. 1905. TYPE: Ecuador. *Sodirol 54/3* (holotype, K; isotypes, P, UC; photos, BM, GH, US ex K). Figure 24. Map 8.

Polypodium oligophlebium Baker in Hook. & Baker, Syn. Fil. 506. 1874, hom. illeg., non Kunze 1850. *Phegopteris oligophlebia* Salomon, Nomencl. 276. 1883, nom. nov. for *Polypodium oligophlebium* Baker, with the same type. *Dryopteris paucinerata* C. Chr., Index Filic. 283. 1905, a nom. nov. for *Polypodium oligophlebium* Baker, with the same type. TYPE: Peru. San Martín: Tarapoto, *Spruce 4653* (holotype, K).

Polypodium coalescens Baker, J. Bot. 15: 164. 1877. *Dryopteris coalescens* (Baker) C. Chr., Index Filic. 258. 1905. TYPE: Ecuador. Pichincha: near San Miguel de los Colorados, Aug. 1875, *Sodirol 54/2* (holotype, K).

Rhizome erect, the internodes approximate, scaly at the apex, the scales 1–3 mm, lanceolate, opaque, brown, rigid, entire; leaves to 1 m; petiole $\frac{1}{2}$ to equaling the lamina, dull brown on both surfaces, scaly, the scales of two types, the smaller type 2–5 mm, opaque, appressed, shiny black abaxially,

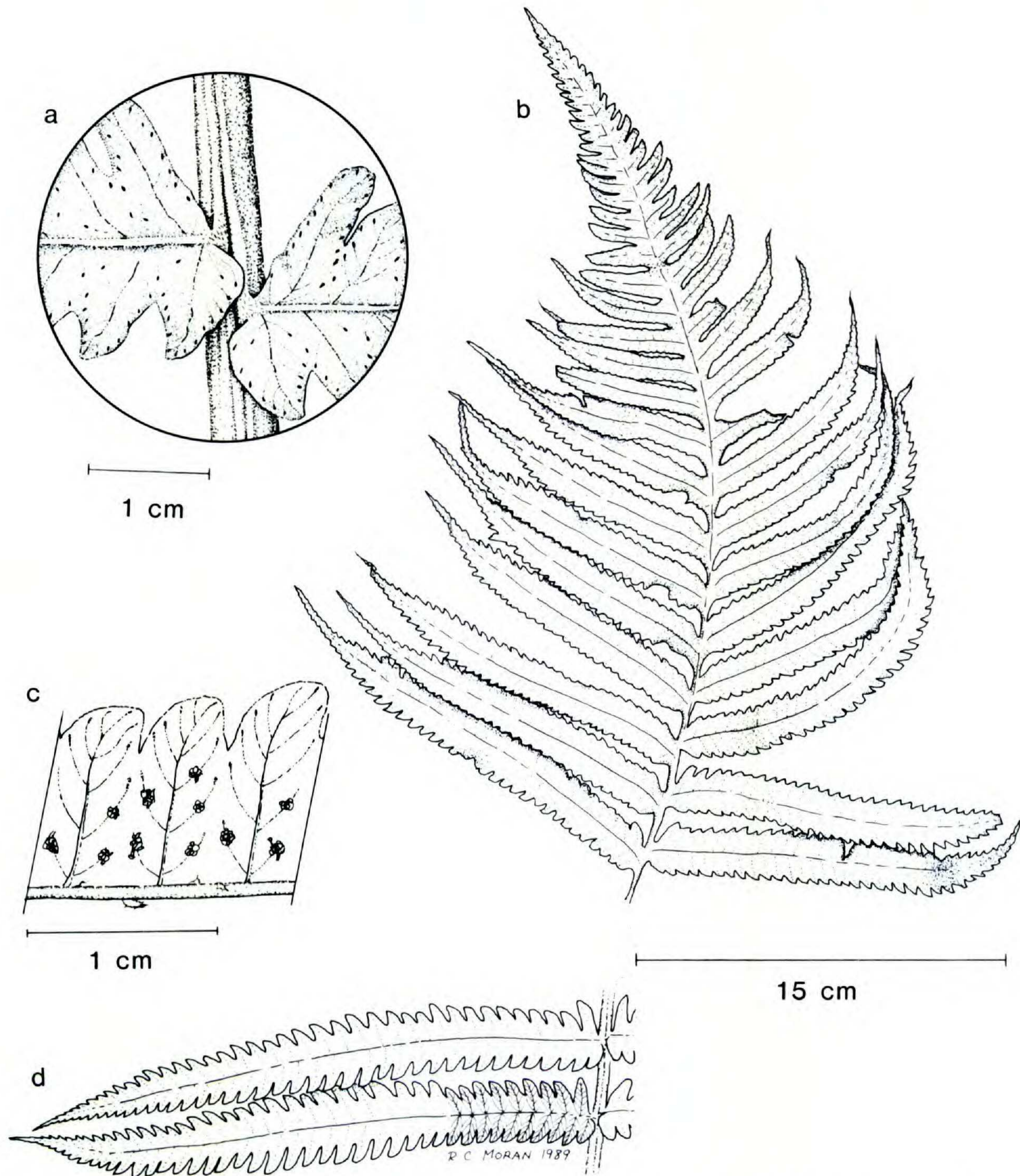
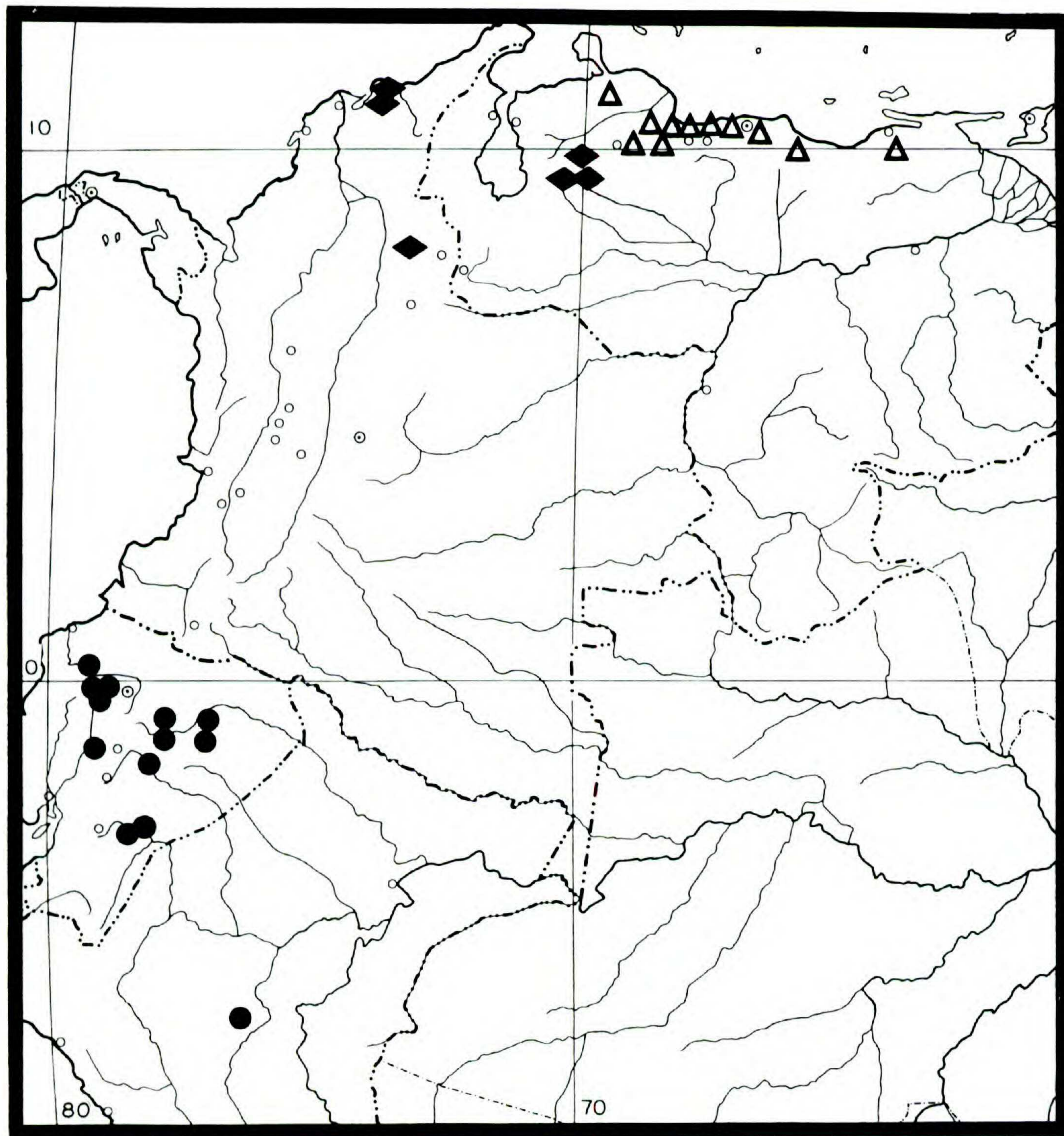


FIGURE 23. *Stigmatopteris nephrodioides*, Funck & Schlim 411 (P; lamina apex, GH).—a. Base of medial pinnae showing the basispicic lobe overlapping the rachis.—b. Distal half of the lamina.—c. Lobes of pinna.—d. Medial pinnae.

entire, ovate-lanceolate, slightly falcate, the larger type 4–9 × 2–4 mm, translucent, spreading, brownish, ovate to lanceolate; lamina 1-pinnate, opaque, the internal glands not visible, oblong-deltate to lanceolate, bulblets lacking; free pinna pairs 4–10; medial pinnae 12–27 × 3–5 cm, widest at or just above the base, the margins entire to crenate, the base sessile, the upper pinnae with a short decurrent base; basal pinnae ca. equaling the suprabasal pinnae, widest near the middle, sessile; rachis brown, the costae stramineous, both axes lacking capitate-glandular hairs, scaly, the scales lanceolate to linear or amorphous; veins reg-

ularly to irregularly anastomosing, those of the sterile leaf with a single, often straight, excurrent vein projecting from the apex where the two lateral veins join; sori variable in shape, round, oblong, or arcuate, lacking an indusial scale.

Additional specimens examined. ECUADOR. COTOPAXI: Quevedo–Latacunga road, km 46 from Quevedo, 600 m, Holm-Nielsen et al. 2906 (AAU, NY, UC). MORONA-SANTIAGO: along new road Mendez–Morona, 650 m, van der Werff & Gudiño 11169 (AAU, F, MO, NY, UC). NAPO: Cordillera Guacamayos, on road Baeza–Tena, ca. 34 km from Baeza, ca. 2,000 m, Øllgaard et al. 35859 (AAU); vic. of Jaguar Hotel, Río Napo, Proctor



MAP 8. Distribution of *Stigmatopteris opaca* (dots), *S. pterorhachis* (diamonds), and *S. nephrodioides* (open triangles).

38712 (NY); ca. 10 km SE of Coca, 250 m, *Harling et al.* 19737 (UC); camino entre Puyo-Tena, casi 10 km S de Río Napo, 500 m, *Moran* 3576 (MO, QCA). PASTAZA: 2 km W of Yuralpa, 440 m, *Holm-Nielsen & Jeppesen* 992 (AAU, NY); Pastaza Canton, 20 km al sur de la población de curary, *Zak & Espinoza* 5287 (MO, QCNE). PICHINCHA: near San Miguel, *Sodirol s.n.*, Jan. 1882 (P, US); Peripa flumine, 300–400 m, *Verleysen* 174 (P); flumen Peripa, Toachi, *Sodirol s.n.* (SI); NE of Vicente Maldo, Reserva de ENESA, 600 m, *Laegaard* 51614 (AAU, MO). ZAMORA-CHINCHIPE: ca. 4 km. E Paquisha, 1,250 m, *Øllgaard et al.* 90435 (AAU, MO).

Stigmatopteris opaca occurs in Ecuador and Peru (Map 8), from 250 to 2,000 m. It is extremely variable in venation and shape of the sori. Although

the veins are always anastomosing, they may do so irregularly (as in the other species with anastomosing veins) or they may do so regularly, with the veinlets straight and producing a single excurrent veinlet where they unite. This latter type of venation is similar to that found in *Thelypteris* subg. *Meniscium*. The sori vary from round to (in the type) arcuate, but some intermediate specimens have shapes between these extremes (Fig. 24b, c, e).

This species may be distinguished from *S. heterophlebia* by its nonpubescent axes and greater number of pinna pairs. It can be distinguished from

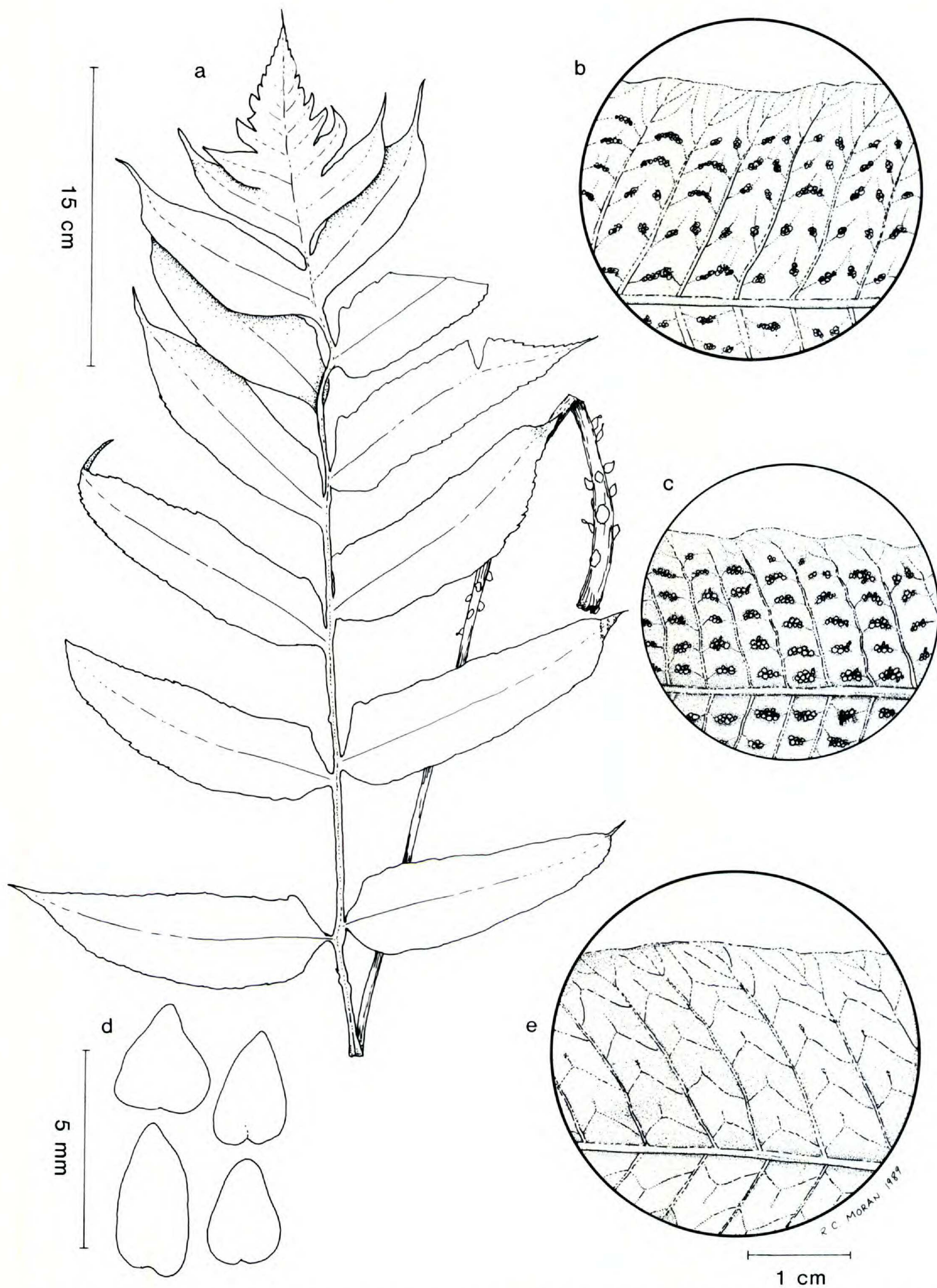
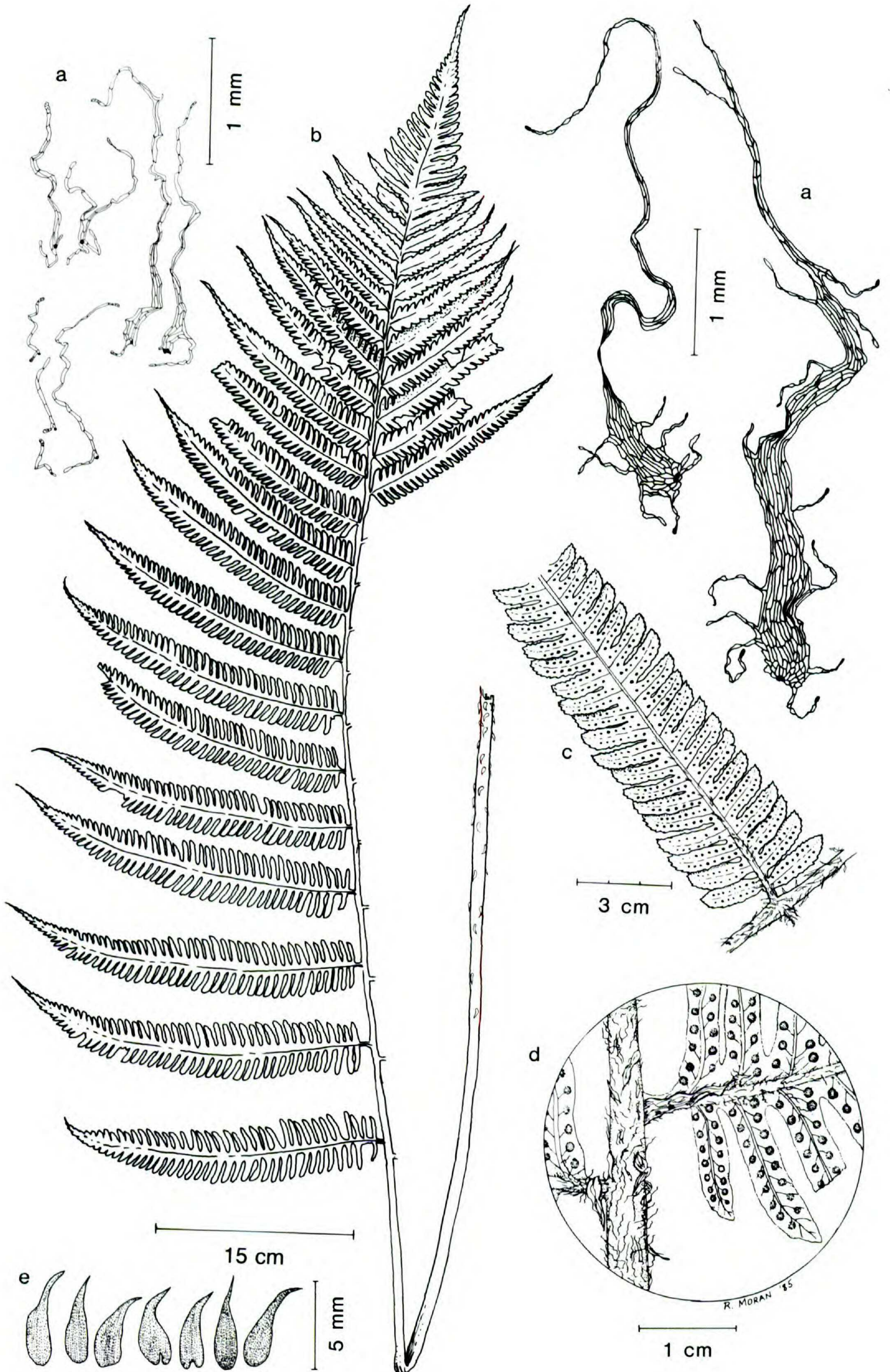


FIGURE 24. *Stigmatopteris opaca*.—a. Leaf (*van der Werff & Gudiño 11169*, MO).—b. Mixed round and arcuate sori (*Moran 3576*, MO).—c. Arcuate sori only (*Sodiro s.n.*, K).—d. Petiole scales (*van der Werff & Gudiño 11169*, MO).—e. Venation of a sterile pinna, showing single excurrent veinlet from vein junctures (*Holm-Nielson et al. 2906*, AAU).

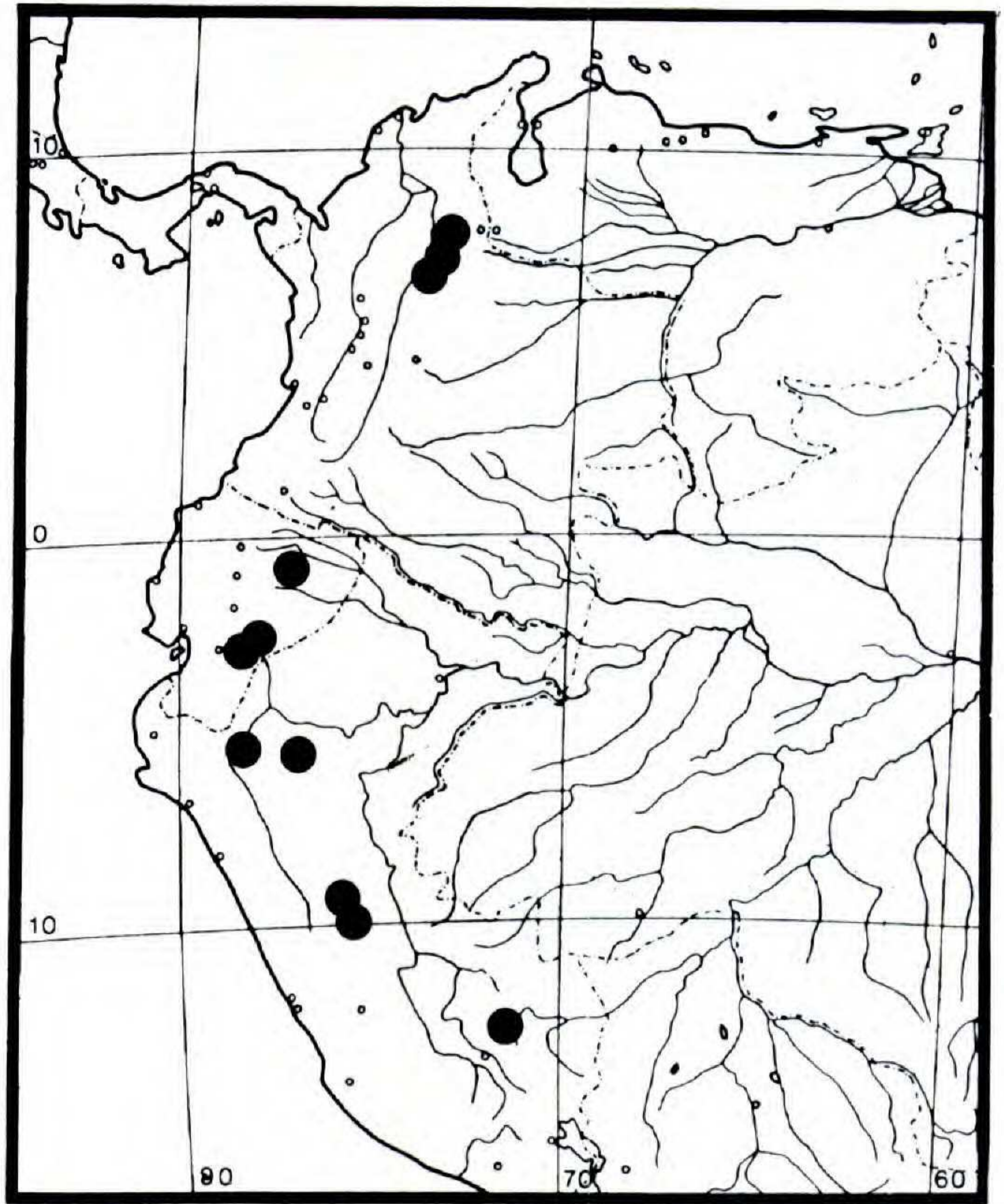


S. killipiana by its brown (not atropurpureous) petiole and rachis, thicker lamina, and tendency for the sori to become arcuate. The lamina is thicker and the glands less visible than in the other species of *Stigmatopteris*.

18. *Stigmatopteris pellucidopunctata* (C. Chr.) C. Chr., Bot. Tidsskr. 29: 304. 1909. *Polypodium macrophyllum* Hook., Sp. Fil. 4: 241. 1862, hom. illeg., non (Blume) Mett. 1856. *Phegopteris macrophylla* (Hook.) J. Smith, Hist. Fil. 233. 1875, hom. illeg., non Mett. 1859. *Dryopteris pellucidopunctata* C. Chr., Index Filic. 283. 1905, nom. nov. for *P. macrophyllum* Hook. TYPE: Peru. San Martín: Mt. Guayrapurima, Aug. 1856, Spruce 4720 (holotype, K; isotypes, BM, G, P, US; photos, F, GH, MO, NY, UC ex BM). Figure 25. Map 9.

Rhizome erect or short-creeping; leaves to 2 m long; petiole $\frac{1}{2}$ to equaling the length of the lamina, brown, scaly, the largest scales $4-6 \times 2-2.5$ mm, lanceolate, falcate, occasionally with darkly sclerified abaxial surfaces, the base cordate (appearing false peltate), with smaller fibrillose scales present, reddish; lamina 1-pinnate-pinnatifid, lanceolate, lacking buds; pinnae $20-40 \times 2.5-6$ cm, 15-20 pairs, cut ca. $\frac{2}{3}$ to the costa, sessile or the basal ones short-stalked, the stalk 2-7 mm; segments 4-10 mm wide, serrate at the apex, the sides entire, serrate or rarely lobed, the basal basisopic segment not reduced; rachis and costae stramineous or brown, scaly, the larger scales nonbullate, lanceolate to linear, mixed with smaller fibrillose ones; veins free, 7-14 per segment, unbranched or 1-forked with a short acroscopic branch that in fertile segments bears the sorus; sori lacking an indusiumlike scale.

Additional specimens examined. COLOMBIA. ANTIOQUIA: Municipio San Carlos, 47.5 km E of San Carlos, Lake Punchina, Quebradas La Villa y El Macho, Brant *et al.* 1679 (MO). SANTANDER: ca. 25 km E of Puerto Wilches, E side of Magdalena Valley, 70-130 m, Elias 8 (US); vic. of Barranca Bermeja, Magdalena Valley, between Sogamoso and Carare rivers, Amarilla Creek, 200 m, Haught 1931 (GH, US). DEPTO. UNKNOWN: no locality, Schlim 1683 (BM). ECUADOR. MORONA-SANTIAGO: along new road Mendez-Morona, 650 m, van der Werff & Gudiño 11170 (MO, QCNE, UC). PASTAZA: Río Pastaza, between Destacamento Chiriboga and Apachi Entza, 285



MAP 9. Distribution of *Stigmatopteris pellucidopunctata*.

m, Øllgaard *et al.* 35212 (AAU). NAPO: 27 km SE of Coca, Pozo Auca 4, 200 m, Moran 3624 (MO, Q, QCA). PERU. AMAZONAS: Provincia de Bagua, Quebrada Tambillo (below km 280 of Marañón road), valley of Río Marañón above Cascadas de Mayasí, 425-525 m, Wurdack 2002 (GH, US, USM). HUÁNUCO: Fundo Chela, Sinchono, Aguilar 927 (USM). MADRE DE DIOS: Provincia Manú, Atalaya, vic. of Hacienda Amazonia, 2-3 km W of village, 500-600 m, Foster & Wachter 7437 (MO, USM). PASCO: Provincia Oxapampa, Paujil, near Puerto Bermúdez, León *et al.* 311 (USM). BOLIVIA. LA PAZ: Provincia Sud Yungas, Chulumani, 107 km NNE pasando Asunta, Alto Charia sobre el Río San José afluente, Río Boopi, 900 m, Beck 8500 (UC).

Stigmatopteris pellucidopunctata grows from Colombia to Bolivia (Map 9), from 100 to 900 m. It is closely related to *S. sordida* and *S. ichthiosma* but may be distinguished by linear to fibrillose scales on the costae and costules (Fig. 25a). The stiff, adaxially sclerified, appressed petiole scales of *S. pellucidopunctata* are of slightly different shape than those of *S. ichthiosma*, being lanceolate and falcate rather than ovate and symmetrical. In Ecuador, *S. pellucidopunctata* occurs only on the eastern side of the Andes, whereas *S. ichthiosma* occurs only on the western side.

FIGURE 25. *Stigmatopteris pellucidopunctata*. —a. Proscapes or microscales (uniseriate) and multiseriate scales from the abaxial surface of the lamina. —b. Leaf. —c. Basal portion of medial pinna. —d. Rachis and costae with linear-lanceolate scales. —e. Petiole scales. a, b, d, e, Moran 3624, MO. c, van der Werff & Gudiño 11170, MO.

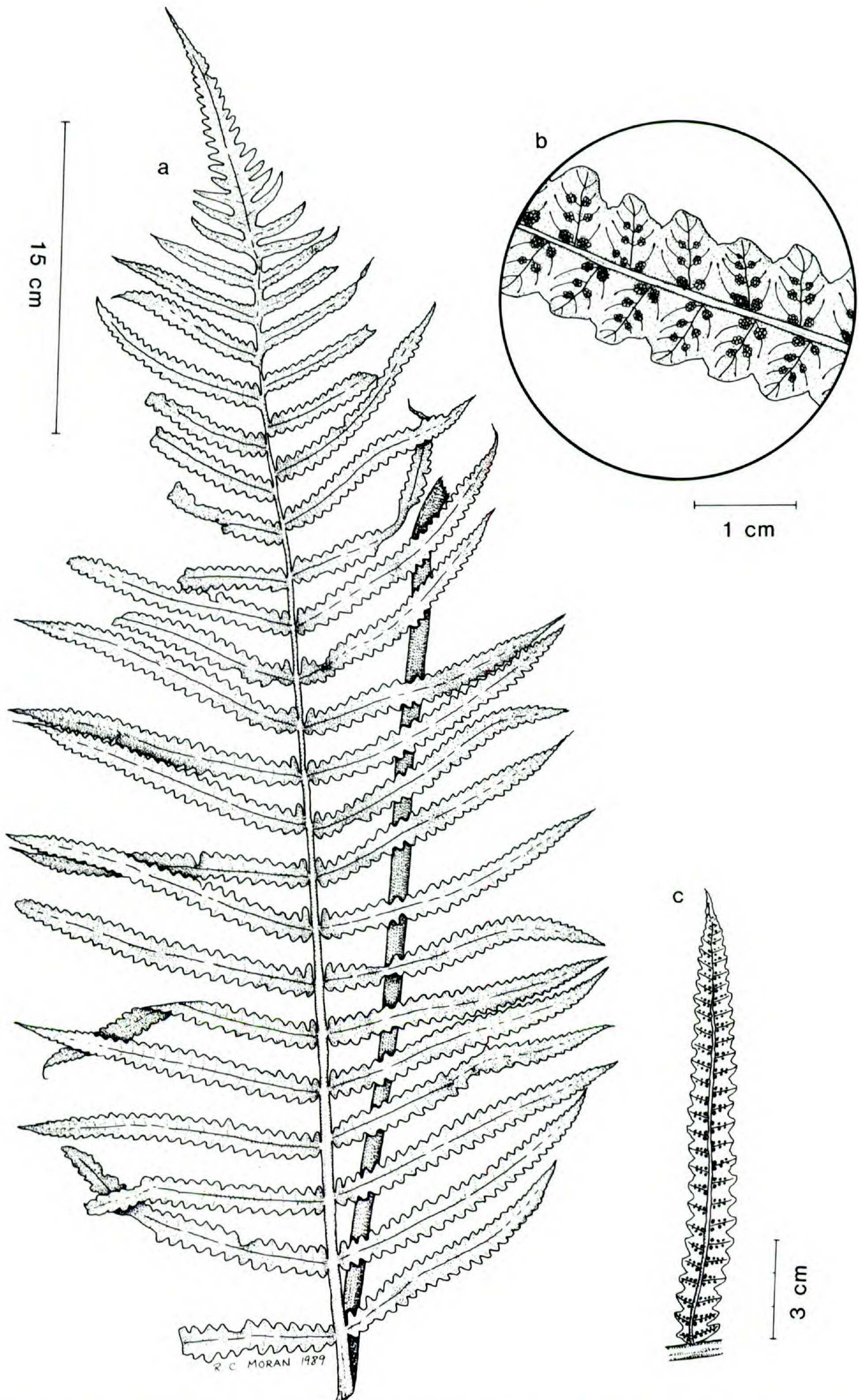
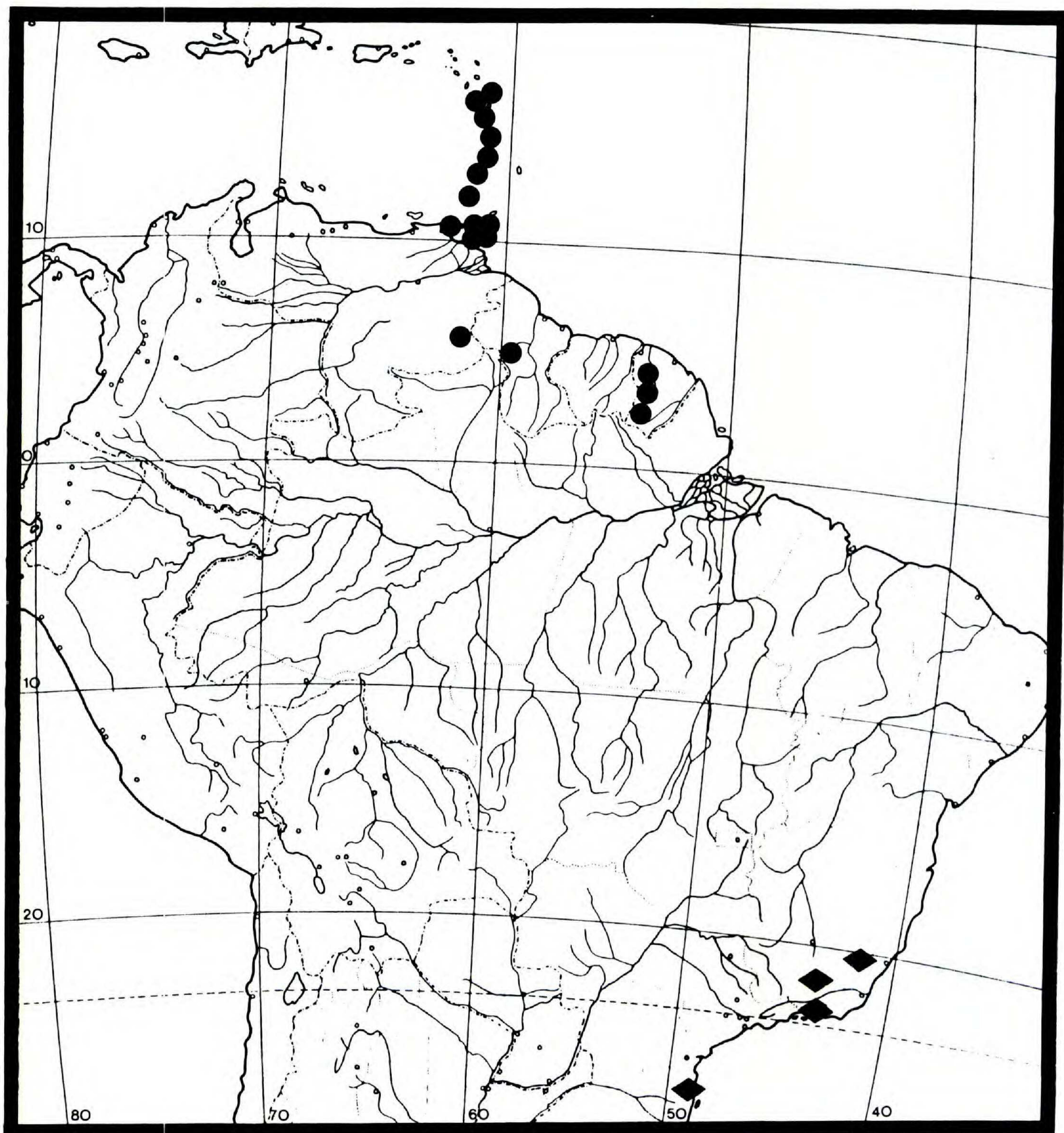


FIGURE 26. *Stigmatopteris prionites*.—a. Leaf (Blanchet 2483, BM).—b. Venation and sori (Martius 305, B).—c. Fertile pinna (Martius 305, B).



MAP 10. Distribution of *Stigmatopteris rotundata* (dots) and *S. prionites* (diamonds).

19. *Stigmatopteris prionites* (Kunze) C. Chr., Bot. Tidsskr. 29: 298. 1909. *Dryopteris prionites* (Kunze) C. Chr., Index Filic. 286. 1905. *Polypodium prionites* Kunze, Flora Beibl. 1: 29. 1839. TYPE: Brazil, from three states, see discussion below: *Martius* 305 (lectotype, here designated, B; isolectotypes, BM, BR not seen, G, K, L, MO, NY; photo, BM ex BR). Figure 26. Map 10.

Stigmatopteris prionites var. *denticulata* (Fée) C. Chr., Bot. Tidsskr. 29: 299. 1909. *Phegopteris denticulata* Fée, Crypt. Vasc. Brésil 1: 100, t. 32, fig. 2. 1869. TYPE: Brazil. Rio de Janeiro: fazenda de Santa

Anna, *Glaziou* 2400 pro parte (holotype, P; isotype, P).

Rhizome short-creeping; leaves to 1.5 m; petiole ca. equaling the lamina, stramineous to brown, scaly at the base, the scales 4–8 × 1–2 mm, brown, thin, lanceolate; lamina 1-pinnate-pinnatifid, lanceolate, lacking buds, only a few distalmost pinnae with short-decurrent bases; pinnae 11–20 × 1.1–2.3 cm, cut ¼–½ to the costa, pairs 19–26, the base sessile or nearly so; segments entire to denticulate at the apex, separated by broad, U-shaped sinuses; rachis and costae stramineous,

sparsely scaly, the scales ovate to lanceolate; veins free, not forked, 3–5 per lobe; sori inframedial; indusial scale absent.

Additional specimens examined. BRAZIL. BAHIA: no locality, *Luschnath* 120 (B), 1836, *Blanchet* 2483 (BM, G, P). ESPÍRITO SANTO: Jatiboca, *Brade* 18405 (G, GH, MO, NY, P). MINAS GERAIS: Juiz de Fora, Rio do Peixe, *Krueger* 17107 (UC); Viçosa, Corrigo Riberro, Agricultural College, 675 m, *Mexia* 4893-a (UC); Distrito Rio Branco, Retiro de Antonio Avelino, 740 m, *Mexia* 5492 (F, GH, K, NY, P, UC, US, Z). STATE UNKNOWN: Mt. Parahyba, 1886, *Goldi* s.n. (G); Brasilia, *Riedel* s.n. (US); no locality, *Glocker* 32 (BM, US).

Stigmatopteris prionites is endemic to southeastern Brazil (Map 10) where it grows in wet forests from 500 to 740 m. It can be distinguished from all other *Stigmatopteris* in Brazil by the combination of narrow (1.1–2.2 cm) pinnae cut up to halfway to the costa, broad, obtuse lobes with wide sinuses, few (3–5) veins per lobe, and inframedial sori. The fertile pinnae are slightly narrower than those of the sterile.

Variety *denticulata* differs by having more deeply lobed pinnae with the lobes denticulate at the apex. Because this character intergrades with plants having entire lobes, the variety is here placed in synonymy.

The type collection has a varied provenance. Although none of the specimens have a more specific locality than "Brazil," the original description by Kunze states that *Martius* 305 comes from the provinces of Bahia (Porto Seguro), Espírito Santo, and Rio de Janeiro. Therefore, I chose the sheet at Berlin (B) as the lectotype.

20. *Stigmatopteris pterorhachis* R. C. Moran, sp. nov. TYPE: Colombia. Magdalena: Santa Marta, Sierra del Libano, 1,800 m, *H. H. Smith* 1045 (holotype, MO; isotypes, BM, DUKE, F, GH, MICH, NY, P, UC, US). Map 8.

Folia 1-pinnata, pinnis 4–7 utroque costae latere, gemmis absentibus; rhachis costaeque abaxialiter glabrae; venae irregulariter anastomasantes.

Rhizome short-creeping, the internodes 0.5–2 cm, scaly at the apex, the scales 1–3 mm, ovate to lanceolate, opaque, brown, rigid, entire; leaves 50–110 cm; petiole ca. equaling the lamina, dull brown or tan on both surfaces, lacking hairs, scaly, the scales 4–9 mm, translucent, spreading, brownish, lanceolate; lamina 1-pinnate, oblong-deltate, bulblets lacking; free pinna pairs (3–)4–7; basal pinnae usually somewhat reduced, widest near the middle, stalked, the stalk 2–4 mm; medial pinnae (10–)15–20 × 2.5–3.5 cm, widest at or near the

base, the margins entire to deeply crenate; distal pinnae with long-decurrent bases; rachis and costae tan, light brown, or stramineous, lacking hairs, scaly, the scales to 1 mm, 1–2 cells wide, filamentous, usually with a long central filament and several shorter ones branched from the point of attachment; veins part free and part anastomosing, the areoles with 1 or 2 curved, irregular or forked excurrent veinlets; sori discrete, indusial scale absent.

Additional specimens examined. VENEZUELA. LARA: Dtto. Morán, 1,500 m, *Rivero et al.* 1602 (PORT, UC); Dtto. Menez, between Cubiro and Escalera, 10–15 km SW of Cubiro, 1,600–2,000 m, *Steyermark et al.* 110227 (F). PORTUGUESA: Dtto. Sucre, Los Paramitos, a 20 km por aire al SO de Biscucuy, 1,000–1,500 m, *Ortega et al.* 1822 (MO, PORT); Dtto. Guanare, ESE of Paraíso de Chabasquén, along road to Cordoba, ca. 27 minutes from Chabasquén, 1,500 m, *A. R. Smith* 1031 (AAU, CR, MO, PORT, UC, Z). COLOMBIA. MAGDALENA: Sierra Nevada, Río Macha, *Schlim* 856 (K, P); Sierra Nevada de Santa Marta, finca Los Arroyitos, 1,600–1,700 m, *Kirkbride* 2377 (NY, UC). NORTE DE SANTANDER: Ocaña, *Schlim* 596 (BM, G, K).

Stigmatopteris pterorhachis occurs in northwestern Venezuela and northern Colombia (Map 8) where it grows primarily in cloud forests from 1,000 to 1,800 m. It greatly resembles *S. heterophlebia*, but differs by the absence of capitate glandular hairs on the axes, the presence of 1- or 2-cells-wide, filamentous, basally branched scales on the costae, and the greater number of pinna pairs. These characters correlate on all specimens except *Rivero et al.* 1602, which is moderately to sparsely glandular on the abaxial surface of the rachis, but lacks glands on that surface of the costae (unlike *S. heterophlebia*). The specimen is typical of *S. pterorhachis* in the other two characters, which separate it from *S. heterophlebia*.

The name *S. alloëoptera* (Kunze) C. Chr. has been previously misapplied to this species and to *S. heterophlebia* (see section on names of uncertain application).

21. *Stigmatopteris rotundata* (Willd.) C. Chr., Bot. Tidsskr. 29: 297. 1909. *Aspidium rotundatum* Willd., Sp. Pl. ed. 4, 5: 247. 1810. *Dryopteris rotundata* (Willd.) C. Chr., Index Filic. 289. 1905. TYPE: Plumier, *Traité Foug. Amér.* 29, t. 38. 1705, illustrating a plant from Martinique. Figure 27. Map 10.

Polypodium flavopunctatum Kaulf., Enum. Filic. 108. 1824. *Phegopteris flavopunctata* (Kaulf.) Fée, Mém. Foug. 11: 51. 1866. SYNTYPES: Martinique, *Sieber* 350 (B, MO; photos, BM, F, G, GH, MO, NY, P, UC ex L); Martinique and Montserrat, *Ryan* s.n. (P-herb. Vahl).

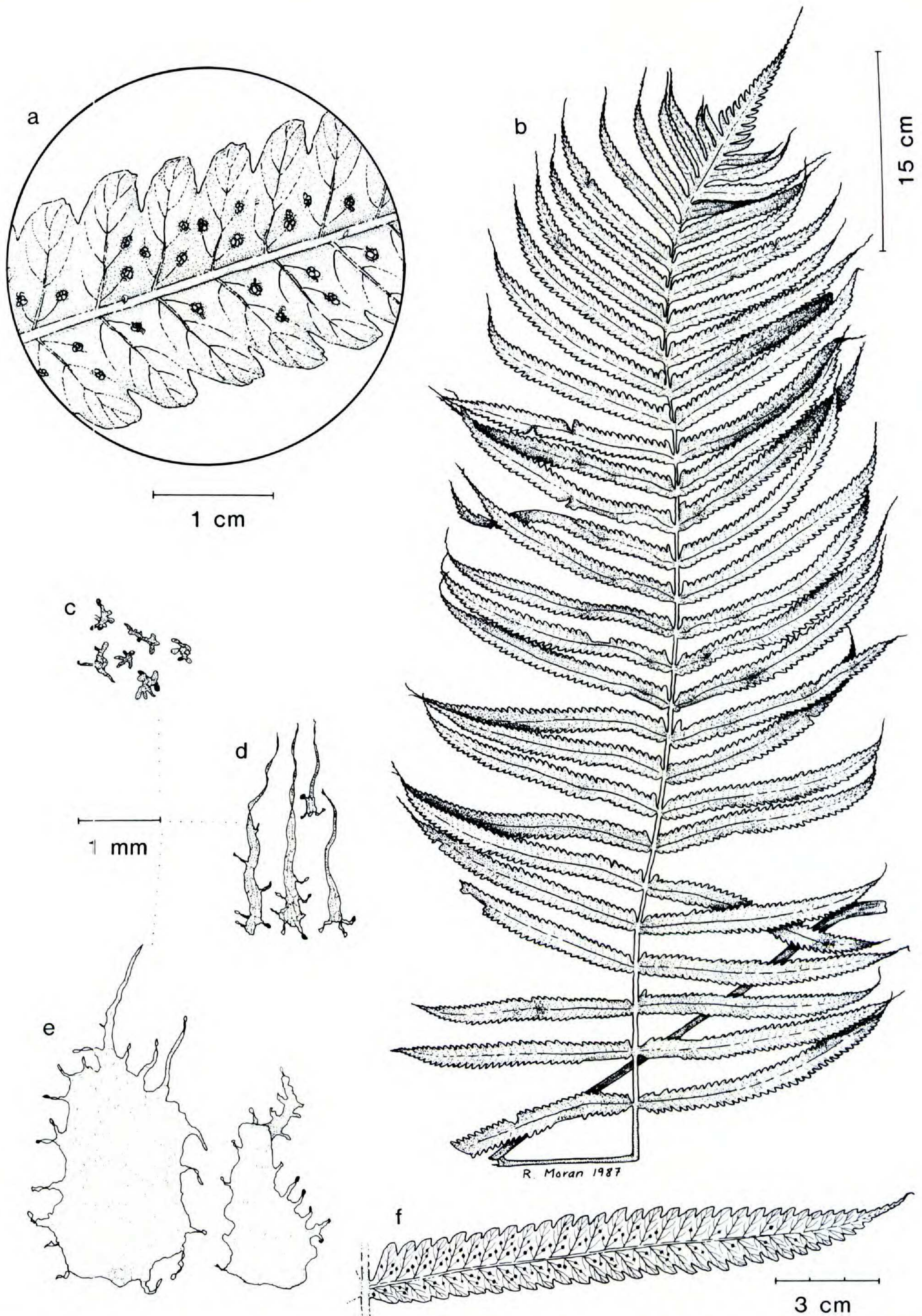


FIGURE 27. *Stigmatopteris rotundata*.—a. Venation and sori (Morton 6184, US).—b. Leaf (Morton 6184, US).—c. Costal scales (Alston 494, NY).—d. Costal scales (collector unknown, K-H1058/87).—e. Costal scales (Duss 4074, NY).—f. Fertile pinna (collector unknown, K-H1058/87).

Stigmatopteris rotundata var. *trinidadensis* C. Chr.,
Bot. Tidsskr. 29: 297. 1909. SYNTYPES: Trinidad.
Fendler 98 (B, BM, GH, K, MO, UC, US); Cabueres
de Sarrapo, 11 Nov. 1863, Hart 3707 (US, NY),

6259 (US) [these two numbers equal the Botanic
Garden Herbarium of Trinidad nos. 337 and 1236,
respectively].

Nephrodium imrayanum Hook., Sp. Fil. 4: 86, t. 242.

1862. *Aspidium imrayanum* (Hook.) Fée, Mém. Foug. 11: 79. 1866. *Dryopteris imrayana* (Hook.) Domin, Rozpr. Král. České Společn. Nauk, -Tr. Mat.-Přír. N.R., 21: 191. 1929. TYPE: Dominica. *Imray 17* (holotype, K; isotype, BM; photos, GH, US ex BM).

Rhizome short-creeping, the scales 2–4 mm, brown, entire, narrowly lanceolate; leaves to 2 m; petiole ½ to equaling the lamina, brown to tan, the scales all of one type, 5–12 × 1–2 mm, lanceolate, translucent, never blackish or thickened, entire, brown; lamina 1-pinnate-pinnatifid, oblong to oblong-lanceolate, lacking bulbils; pinnae 11–26 × 1.5–2.5(–3) cm, 18–32 pairs, linear or rarely narrowly lanceolate, crenate or cut less than ⅓(–½) to the costa; upper pinnae adnate to the rachis and confluent only in the distal ¼–⅓ of the lamina, the lower pinnae sessile or stalked, the stalk to 8 mm; rachis and costae scaly, the scales ovate to lanceolate, filiform, or roundish to ovate and irregularly lobed; veins free, 3–4 per segment; sori lacking an indusiumlike scale, inframedial to suprasedial, those on the basal veinlets often at the apex of the vein.

Additional specimens examined. GUADELOUPE. Morne du Calababbaye, *Belanger 821* (G); no locality, *Duss 80* (US); Bon du Marne de la Madeleine, Trois Rivières, *Duss 729* (P); Bois de la Calebasse, 450–900 m, *Duss 1561* (NY, P); Bois de la cascade de Vanchelet, 330–960 m, *Duss 4074* (NY, US); Forêt du Nez bassé, 1,000 m, *Le Gallos 2965* (P), *3100* (P); *L'herminier 115* (B, G, GH); no locality, *Marie 516* (F, G, P); Basse Terre, above Matouba, *Proctor 20345* (GH); Ravine Roche, *Questel 2905* (US); Gran Etang, 350 m, *Stehlé 1104* (US); ravine Malanga, 680 m, *Stehlé 1463* (US); Bains Jaunes, 1,050 m, *Stehlé 1887* (US). DOMINICA. Lagunem Roseau, *Eggers 905* [Toepffer no. 668] (B, G, P); Sylvania estate, 488 m, *Hodge 103* (GH, MO, NY, UC, US); Lisdara, *Hodge 104* (GH, US); Lisdara, 470 m, *Hodge 2377* (GH, NY, US); 1 mi. E of Laudat, ca. 665 m, *Hodge & Hodge 1972* (GH); no locality, *Imray 39* (B); St. Paul Parish, 0.5 mi. S of Pont Cassé, *Lellinger 362* (MICH, US); St. Paul Parish, *Lellinger 367* (DUKE, GH, US); St. Joseph Parish, S of Tiperie, N side of Morne Couronne, *Lellinger 507* (US); Mt. Diablotin, *Lloyd 902* (NY, US); St. John, Morne Diablotin, *Webster 13329* (DUKE, US); St. Joseph, ridge S toward McFarlin, *Webster 13566* (US), *13558* (MO, UC, US); above Bellevue along trail to Grand Bay, *Wilbur 7882* (DUKE). MARTINIQUE. No locality, *Belanger 821* (BM, K); Bois du Lorrain, *Duss 1561* (US); no locality, *Hahn 37* (B, BM, P); St. Denis, *Stehlé 3303* (US); Colson, 560 m, *Stehlé 4807* (US); Rivière Dumanée, 600 m, *Stehlé 4883* (UC, US); Bois de la Pirogue, Lorrain, 280 m, *Stehlé 6725* (US); Morne Rouge, 500 m, *Stehlé 7238* (US); vallée du Lorrain, 650 m, *Stehlé 8436* (MICH, US). ST. LUCIA. Mt. Gimie, *Box 1966* (BM). ST. VINCENT. No locality, *Checkley 7* (B); Charlotte Parish, Montreal, *Cooley 8325* (GH); no locality, *Eggers 6869* (F, US); along Chateaubelair River, 300–400 m, *Morton 5373* (GH, US); upper valley of Richmond River, 330–540 m, *Morton 6184*

(US); no locality, *H. H. Smith & G. W. Smith 659* (B, BM, CM, GH). GRENADA. No locality, *Eggers 6164* (F, UC, US); St. Mark Parish, NW slope of Mt. St. Catherine, *Proctor 17244* (MICH, US); no locality, Oct.–May 1890–91, *Sherring s.n.* (BM, K, US). TRINIDAD. Mount Touche, *Britton et al. 1361* (F, NY, US); Morne Bleu, *Britton et al. 2250* (GH, NY, US); Maracas, *Broadway 5355* (BM, F, G, MO, NY, Z); Maracas Road to the bay, N via Santa Cruz, *Broadway 6123* (BM, MO); *Fendler 98* (B, BM, G, GH, K, MO, NY, UC, US); Morne Bleu, road near summit, *Johnston 303* (BM); Morne Bleu, Arima–Blanchisseuse road, *McCallum 104* (BM); Asa Wright Nature Centre, 7 mi. N of Arima, *Mickel 9412* (NY, UC); no locality, *Prestoe 214* (MO). FRENCH GUIANA. Montagne de l'Inini, zone centrale, 750 m, *Cremers 9113* (UC), *9140* (UC); Mt. Galbao, secteur Est, 3°36'N, 53°17'W, 600 m, *de Granville 8873* (UC); Montis Diabolis, in 1847, *Leprieur 270* (P). GUYANA. Ereugfaru, Maiewac River, along the Santa María trail, *Alston 494* (K, NY); Potaro River, 1899, *Jenman s.n.* (NY). VENEZUELA. BOLÍVAR: región de Urimán, 760 m, *Bernardi 938* (PORT); Uei-Tepui, between Luepa and Cerro Venamo, 1,100–1,300 m, *Steyermark & Nilsson 314* (NY, VEN). SUCRE: península de Paria, W de Cerro Humo, 700–750 m, *Steyermark & Rabe 96115* (NY, VEN).

Stigmatopteris rotundata, the type of the genus, occurs from 280 to 1,300 m in the Lesser Antilles, Guianas, and eastern Venezuela. Proctor (1977) listed this species from Montserrat and Kramer (1978) listed it from Suriname (*Versteeg 315*), but I have not seen a specimen from those countries.

The scales in *S. rotundata* are extremely variable. Most plants from the Lesser Antilles have filiform to lanceolate scales (Fig. 27d), but plants from Guadeloupe and (often) Dominica have 2–4-mm-long, broadly ovate, flaccid scales (Fig. 27e). Plants from South America have scales that are less than 1 mm long, roundish to ovate, and irregularly lobed (Fig. 27c). Because no other characteristics other than geography correlate with scale type, I feel it is best only to mention this variation rather than formally name it.

22. *Stigmatopteris sordida* (Maxon) C. Chr., Index Filic. Suppl. 3: 175. 1934. *Dryopteris sordida* Maxon, Contr. U.S. Natl. Herb. 24: 60. 1922. TYPE: Guatemala. Alta Verapaz: near Cubilquitz, 350 m, *von Türckheim 1432* (holotype, US; isotype, US). Figure 28. Map 11.

Stigmatopteris litoralis Rosenstock, Repert. Spec. Nov. Regni Veg. 22: 12. 1925. TYPE: Costa Rica. Limón: Finca Gebr. Hundrisser, *Brade & Brade 353* (holotype, S? not seen).

Rhizome short, ascending; leaves to 1.3 m; petioles ½ to about equaling the lamina, stramineous, tan or brown, the scales 3–10 × 1–2 mm, ovate

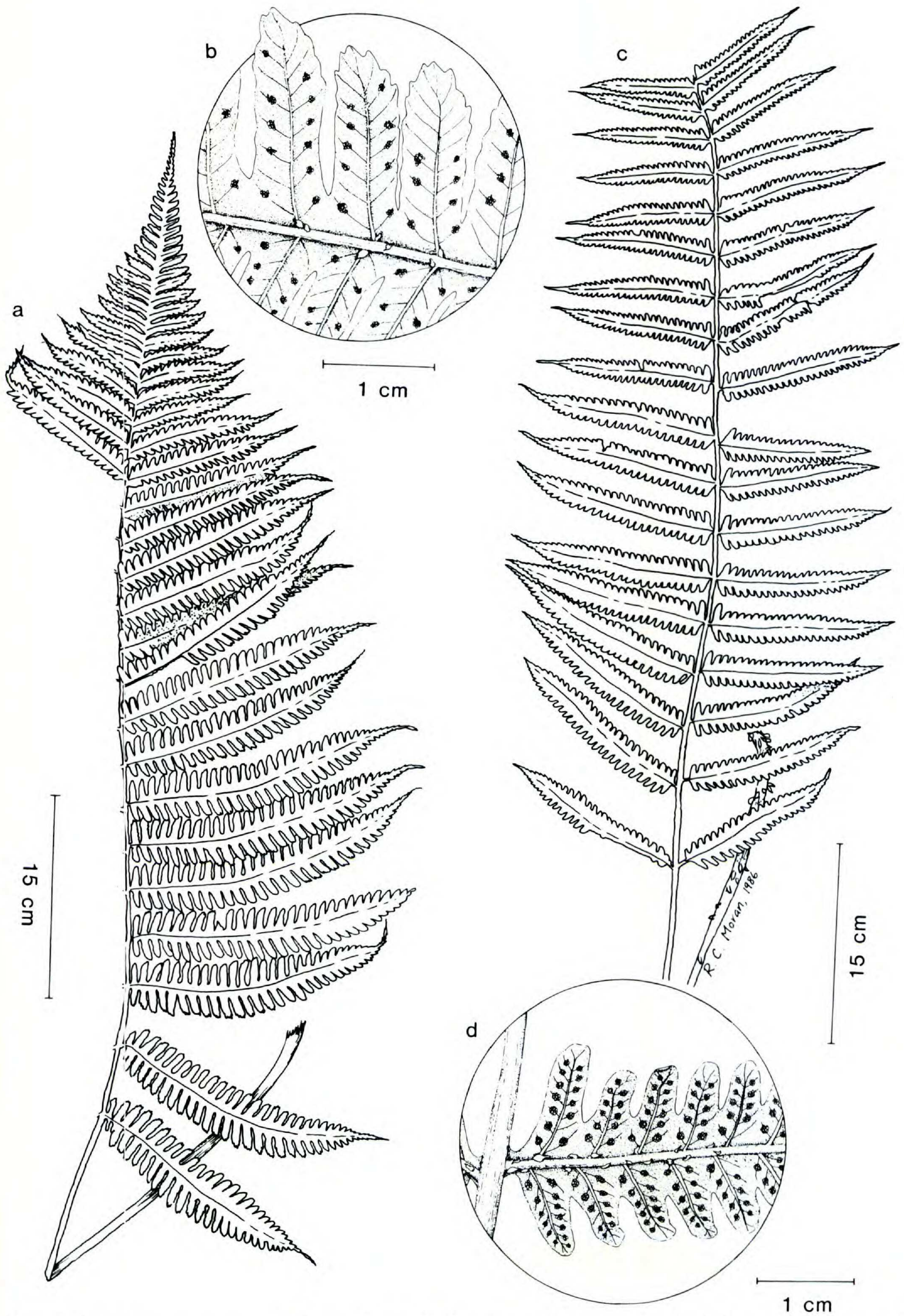
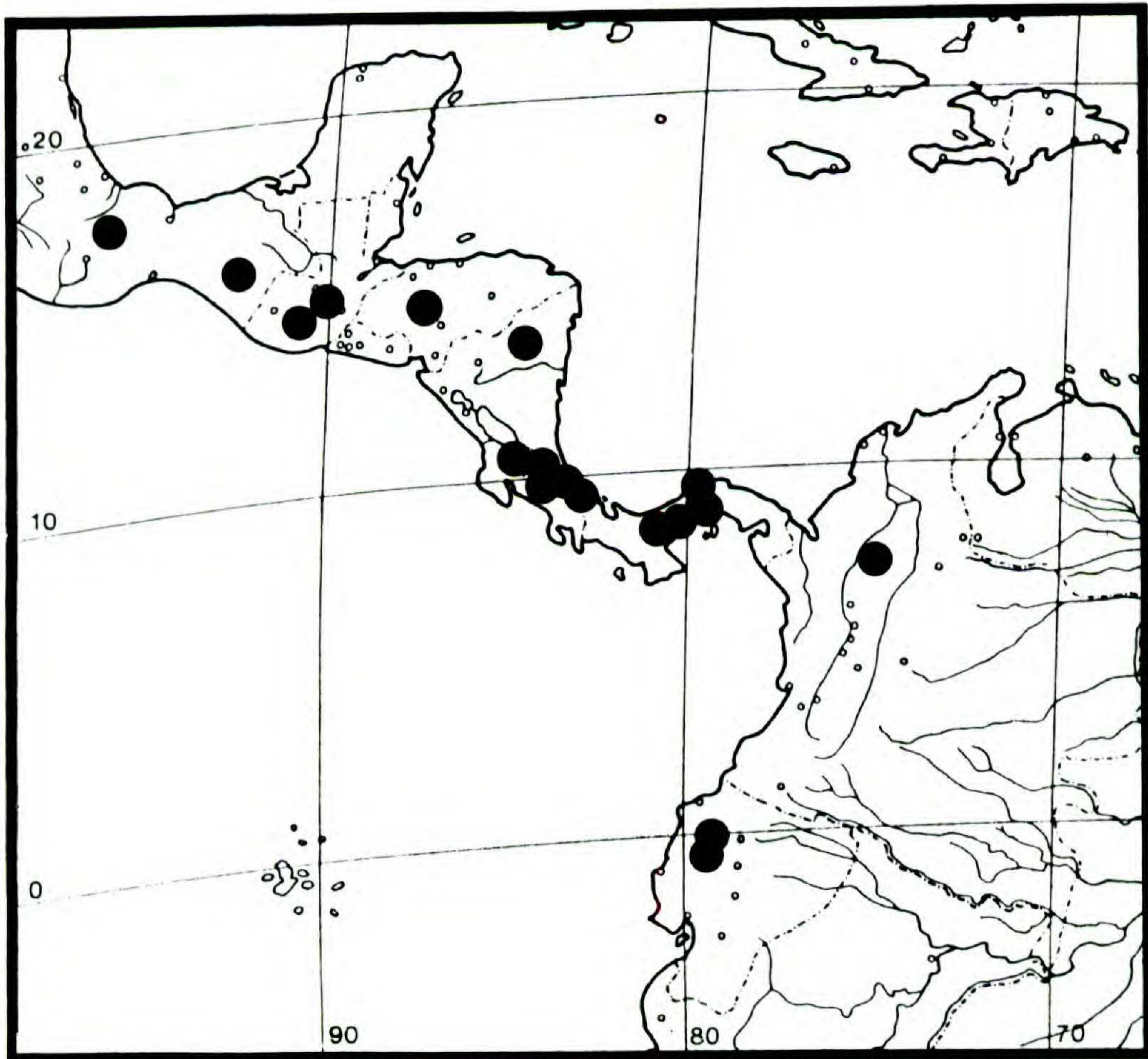


FIGURE 28. *Stigmatopteris sordida*.—a. Leaf.—b. Venation and sori.—c. Leaf.—d. Venation and sori. a, b, Moran 3607, MO. c, d, Moran 3115, MO.

MAP 11. Distribution of *Stigmatopteris sordida*.

to lanceolate, or lanceolate with an attenuate apex, entire, dark brown or rarely (in Colombia) yellow-brown; lamina 1-pinnate-pinnatifid, ovate, lanceolate, or narrowly long-triangular, buds lacking, only the distalmost pinnae with short-decurrent bases; pinnae 15–28 × 2–4 cm, usually cut between $\frac{1}{2}$ – $\frac{3}{4}$ of the way to the costa or sometimes more in the enlarged basal pinnae, pairs 16–25, the basal ones stalked, those above gradually becoming sessile then adnate, the basal basiscopic lobe not overlapping the rachis (although sometimes adnate to it), the basal acroscopic lobe often prolonged; lobes rounded, entire or serrate at the apex; rachis and costae stramineous or the rachis brown, or sparsely scaly, the scales ovate to lanceolate; veins generally 7–10 per lobe, unbranched or rarely with a short acroscopic branch; sori medial, lacking an indusiumlike scale.

Additional specimens examined. MEXICO. CHIAPAS: Finca Mexiquito, *Purpus* 6870 (BM, F, GH, MO, NY, UC, US); no locality, *Purpus* 7256 (GH). OAXACA: Dto. Ixtlán, 29 km S of Valle Nacional, 80 km N of Ixtlán de Juárez, trail E of Rte. 175 at Campamento Vista Hermosa toward Ladú, 500–850 m, *Mickel* 6403 (NY, UC). GUATEMALA. SUCHITEPÉQUEZ: S slope of Volcán Atitlán, Finca Mocá, Guatalon, ca. 250 m, *Hatch & Wilson* 346 (US). HONDURAS. COMAYAGUA: Aldea de "Varsovia," 24 km SE del lago de Yojoa, 600 m, *Claros* 73 (MO).

NICARAGUA. ZELAYA: Costado sur del Cerro La Pimienta y N del Cerro Hormiguero, a Orilla del Caño Hormiguero, 800–900 m, *Grijalva* 290 (MO). COSTA RICA. ALAJUELA: near Río San Rafael, 2 km W of La Marina, Llanura de San Carlos, 550 m, *Molina R. et al.* 17321 (CR, NY); 11 mi. NW of Zarcero, 850 m, *Croat* 43598 (CR, MO); W of Marina, 500 m, *Burger & Stolze* 5055 (CR, F, MO), 5057 (CR, F, GH, NY, US); between San Lorenzo and Los Angeles de San Ramón, above Río San Lorenzo, 620 m, *Burger & Antonio* 11179 (CR, F); Río Chiquito, ca. 40 km on road to Upala, 800 m, *Gómez* 18641 (MO, UC). CARTAGO: E of Turrialba, 900 m, *Lellinger & White* 1428 (CR, MO, US). HEREDIA: Finca La Selva, Puerto Viejo de Sarapiquí, ca. 60–80 m, *Grayum* 2641 (UC); Cerro Sardinal, ca. 2–2.5 km N of Chilamate de Sarapiquí (Finca La Martita), 80–160 m, *A. R. Smith et al.* 1813 (UC); between Río Peje and Río Guácimo, 230 m, *Grayum & Jacobs* 3598 (MO); Finca La Selva, OTS Field Station, 100 m, *Hammel* 11495 (MO), 12382 (CR, MO). LIMÓN: Dist. Talamanca–Canton, ca. 3 km SW of Suretka, near RECOPE test drill site, 70 m, *Moran* 3115 (CR, F, MO); Talamanca, Bri-Bri, *Ocampo S.* 1771 (CR). SAN JOSÉ: Parque Nacional Braulio Carrillo, Fila Carrillo, 600–700 m, *Chacón* 319 (AAU, MO, UC); 25 km S of Villa Mills on the way to San Isidro on the Interamerican Highway, ca. 1,450 m, *Mickel* 3283 (NY, US). PANAMA. CANAL ZONE: Barro Colorado Island, *Kenoyer* 34 (US); Barro Colorado Island, *Knight s.n.* (US); Parque Nacional Soberanía, camino del Oleoducto, *Vásquez* 188 (MO, US). COCLÉ: road to Coclesito, logging camp, 12 mi. from Llano Grande, *Churchill et al.* 4089 (MO); El Valle de Antón, 1,000 m, *Alston* 8744 (BM). COLOMBIA. ANTIOQUIA: Municipio de Zaragoza, Corregimiento de Provedencia, 500–

650 m, *Soejarto & Villa 2685* (COL, GH). ECUADOR. LOS RÍOS: Río Palenque Science Center, 56 km N of Quevedo, *Moran 3607* (MO, QCA, QCNE), *Grayum & Zamora 9376* (MO). PICHINCHA: NE of Vicente Maldonado, Reserva de ENDESA, 600 m, *Laegaard 51610* (AAU).

Stigmatopteris sordida occurs from southern Mexico to Ecuador (Map 11) from 70 to 1,450 m. Maxon (1922), in his original description of this species, stated that the ultimate segments are never serrate, but the type has some serrations on the sterile segments. Specimens that have been collected since 1922, from Central and South America, show that the segment margins vary from entire to serrate. The specific name is derived from the Latin word *sordidus*, meaning dirty-looking, dingy, or soiled. I am uncertain what this refers to.

Although I did not see the type, *S. litoralis* is put here in synonymy because of the original description and because the type was collected from the Atlantic lowlands of Costa Rica where *S. sordida* is common. *Stigmatopteris longicaudata* also grows in the Atlantic lowlands but can be excluded from consideration because the original description of *S. litoralis* stated that the pinnae are cut $\frac{3}{4}$ to the costa and only the distalmost pinnae are short decurrent—characteristics unlike *S. longicaudata*.

23. *Stigmatopteris tyucana* (Raddi) C. Chr., Bot. Tidsskr. 29: 298. 1909. *Polypodium tyucanum* Raddi, Opusc. Sci. 3: 288. 1819. *Dryopteris tijuccana* (Raddi) C. Chr., Index Filic. 298. 1905. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro, Gavia, Mt. Tijuca, *Raddi s.n.* (holotype, FI or PI not seen). Figure 29.

Aspidium brachyneuron Fée, Crypt. Vasc. Brésil 1: 133. 1869. TYPE: Brazil. Bahia: *Blanchet s.n.* (P? not seen).

Phegopteris tenuis Fée, Crypt. Vasc. Brésil 1: 99, t. 30, fig. 1. 1869. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro, *Glaziou 964* (holotype, P).

Rhizome short-creeping; leaves to 1.2 mm; petiole ca. equaling the lamina, stramineous to brown, scaly at the base, the scales 5–12 × 1–2 mm, brown, thin, lanceolate; lamina 1-pinnate-pinnatifid, lanceolate, lacking bulblets, only a few distalmost pinnae with short-decurrent bases; pinnae 12–20 × 2.5–4 cm, 12–15 pairs, cut $\frac{1}{3}$ – $\frac{1}{2}$ to the costa, the base sessile or nearly so, the basal pinnae short-stalked; segments entire; rachis and costae stramineous, sparsely scaly, the scales ovate to lanceolate; veins free, not forked, 4–7 per lobe; sori medial to supramedial; indusial scale absent.

Additional specimens examined. BRAZIL. RIO DE JANEIRO: Colonia Leopoldiana, 1836, *Blanchet 2483* (BM); Terezópolis, Ilindinho, 450 m, *Brade 9972* (GH, UC); Teresópolis, *Brade 9977* (NY); Rio de Janeiro, *Gaudi-chaud s.n.* (G); Petrópolis, Cascatinha, *Glaziou 7245* (B, K, P, US); no locality, *Martius s.n.* (B). SÃO PAULO: Alto da Serra, *Brade 5892* (NY, UC); Serra do Mar, 300 m, *Wacket 50* (NY, UC); Alto da Serra, Parque Cajurú da estacion biológica, *Wacket 21149* (BM, NY, UC), *Luederwaldt 21149* (GH, UC). STATE UNKNOWN: near Rio de Janeiro and Bahia, *Webb s.n.* (MICH); no locality, *Riedel s.n.* (B, GH).

Stigmatopteris tyucana is endemic to southeastern Brazil where it grows in wet forests from 300 to 400 m. The specific epithet is usually spelled *tijuccana*. I prefer to spell it *tyucana* because that was Raddi's original spelling, and the *Code* (Greuter et al., 1988) recommends the use of the author's original spelling (when not in error).

Although I have not seen the type, I am confident from Raddi's excellent illustration (1825, t. 37) and description that the name is here applied correctly.

24. *Stigmatopteris ulei* (Christ) Sehnem, Fl. Illust. Catar. IASPI: 100, est. 25, fig. 2. 1979. *Phegopteris ulei* Christ, Bull. Herb. Boissier sér. 2, 2: 634. 1902. *Dryopteris ulei* (Christ) C. Chr., Index Filic. 299. 1905. TYPE: Brazil. Santa Catarina: município de São Francisco do Sul, Serra de Laranjeira, *Ule 70* pro parte (holotype, P? not seen).

Lamina 1-pinnate-pinnatifid, apparently lacking buds; pinnae cut ca. $\frac{2}{3}$ to the costa, the distal ones (presumably) lacking a basal basisopic lobe adnate to the rachis; the lobes nearly entire, separated by broad, U-shaped sinuses; veins free, 5–8(–10) per lobe; sori inframedial.

I have the type number from P of *Ule 70*, but the locality given on the sheet (im schattigen Urwald der Peninsula da Gloria, Feb. 1884) is different from that given in Christ's original description. The specimen is *Stigmatopteris caudata*. The only specimen that I have seen of *S. ulei* is the photograph of a medial pinna in Sehnem (1979). Because I have not seen a herbarium specimen, the above description is incomplete. *Stigmatopteris ulei* is included in the key and the species descriptions, rather than the uncertain taxa section, to call attention to this poorly known species and because, on the basis of Sehnem's photograph, it appears distinct.

Christensen (1913) thought that this species was probably a form of *S. prionites*, but *S. ulei* is intermediate in cutting—perhaps a hybrid?—be-

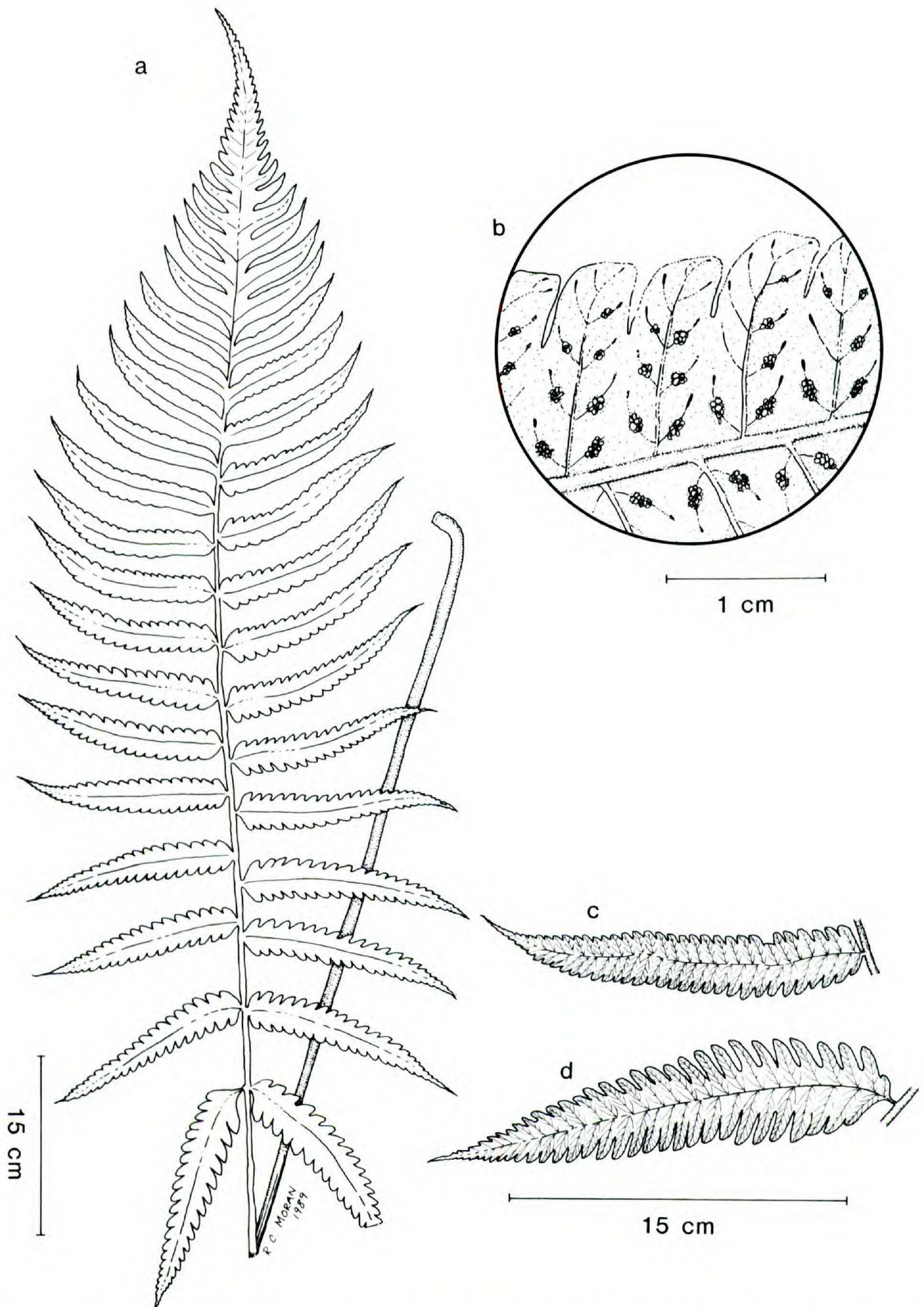


FIGURE 29. *Stigmatopteris tyucana*. —a. Leaf (redrawn from Raddi, 1825, t. 37; scale approximate). —b. Veins and sori. —c. Medial pinna (Brade 9977, NY). —d. Basal pinna (Brade 9977, NY).

tween *S. caudata* and *S. brevinervis*. The intermediate cutting is evident in Sehnem's (1979) photograph, which has *S. ulei* placed between *S. caudata* and *S. brevinervis*. Sehnem (1979) cited the following specimen for *S. ulei*: Brazil. Paraná: Paranagua, Morro de Tabaquara, terrícola na mata pluvial de encosta de morro, 50–100 m, Hatsch-

bach & Imaguire 16361. Obviously, it is difficult to assess whether *S. ulei* represents a hybrid without having specimens for study.

EXCLUDED TAXA

Dryopteris subg. *Stigmatopteris*, group *Peltochlaena*
Fée ex C. Chr., Kongel. Danske Vidensk. Selsk.

- Skr., Naturvidensk. Afd. ser. 7, 10: 74. 1913. = *Cyclodium* C. Presl (fide Smith, 1986).
- Stigmatopteris clypeata* (Maxon & C. Morton) Lellinger, Proc. Biol. Soc. Wash. 89: 730. 1977. = *Thelypteris clypeata* (Maxon & C. Morton) Kramer (fide Kramer, Acta Bot. Neerl. 18: 141. 1969).
- Stigmatopteris guianensis* (Klotzsch) C. Chr., Index Filic. Suppl. 3: 173. 1934. = *Cyclodium guianense* (Klotzsch) A. R. Smith (fide Smith, 1986).
- Stigmatopteris meniscioides* (Willd.) Kramer in Kramer & van Donselaar, Koninkl. Nederl. Akad. Wetensch. Proc. 71: 521. 1968. = *Cyclodium meniscioides* (C. Morton) A. R. Smith (fide Smith, 1986).
- Stigmatopteris paludosa* (C. Morton) R. Tryon & A. Tryon, Rhodora 83: 136. 1981. = *Cyclodium meniscioides* var. *paludosum* (C. Morton) A. R. Smith (fide Smith, 1986).
- Stigmatopteris sancti-gabrielii* (Hook.) C. Chr., Index Filic. Suppl. 3: 175. 1934. = *Cyclodium guianense* (Klotzsch) A. R. Smith (fide Smith, 1986).
- Stigmatopteris varians* (Fée) Alston, Kew Bull. 1932: 309. 1932. = *Cyclodium varians* (Fée) A. R. Smith (fide Smith, 1986).

NAMES OF UNCERTAIN APPLICATION

Stigmatopteris alloëoptera (Kunze) C. Chr., Bot. Tidsskr. 29: 300. 1909. *Polypodium alloëopterum* Kunze, Linnaea 25: 748. 1835. TYPE: Venezuela. Distrito Federal: near Galipán, 1,200–1,500 m, Sep., *Wagner 460* (LZ—destroyed).

This name does not represent *S. heterophlebia* or *S. pterorhachis* (previously treated as one), to which it was applied by all previous pteridologists. There are three reasons why this former application cannot stand. First, Kunze described the pinnae of *Polypodium alloëopterum* as deeply incised-crenate, yet the pinnae of the former two species are only entire to deeply crenate. Second, Kunze likened the leaf of *S. alloëoptera* to that shown in Raddi's plate of *S. tyucana*; yet *S. tyucana* lacks the broad, decurrent, pinna bases that are distinctive for *S. heterophlebia* and *S. alloëoptera*. In addition, Raddi's plate clearly shows a leaf with deeply lobed pinnae and free veins. Third, *S. heterophlebia* and *S. pterorhachis* have never been found in the coastal mountains around Caracas where the type was collected—this despite much collecting activity in that area.

The only species of *Stigmatopteris*—and a common one—which occurs around Caracas is *S. nephrodioides*. This species has deeply lobed pinnae, free veins, and is like the leaf pictured in Raddi's plate. I strongly suspect, but cannot prove, that *P. alloëoptera* applies to *S. nephrodioides*, the later name. I do not, however, want to replace the well-known name *S. nephrodioides* with *S. alloëoptera* because I have not seen the type of *S. alloëoptera* and because *S. nephrodioides* has been widely used.

Phegopteris perforata Fée, Mém. Foug. 5: 248. 1852. TYPE: Country and collector unknown (P—herb. Mougeot).

Christensen (1920), who apparently saw the type, said that this name applied to a species of *Stigmatopteris* and was “badly described on an imperfect specimen of unknown origin. The name ought to pass into oblivion.” Among Fée's specimens received from Paris (P), I did not see any specimens with this name.

LITERATURE CITED

- CHRISTENSEN, C. 1909. On *Stigmatopteris*, a new genus of ferns with a review of its species. Bot. Tidsskr. 29: 291–304.
- . 1913. A monograph of the genus *Dryopteris*. Part 1. The tropical American pinnatifid-bipinnatifid species. Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. ser. 7, 10: 55–282.
- . 1920. A monograph of the genus *Dryopteris*. Part 2. The tropical American bipinnate-decompound species. Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. ser. 8, 6: 3–132.
- FARRIS, J. S. 1988. HENNIG86. Version 1.5 [photocopy of documentation accompanying program].
- GREUTER, W. et al. 1988. International Code of Botanical Nomenclature. Regnum Veg. 118: 1–328.
- HOLTUM, R. E. 1968. Flora of Malaya, Volume 2. Ferns. Government Printing Office, Singapore.
- . 1984. Studies of fern genera allied to *Tectaria*, I. A commentary on recent schemes of classification. Fern Gaz. 12: 313–319.
- KRAMER, K. U. 1978. The pteridophytes of Suriname. Uitgaven Natuurw. Studiekring Suriname Ned. Antillen 93: 1–198.
- MAXON, W. R. 1922. Studies of tropical American ferns—No. 7. Contr. U.S. Natl. Herb. 24: 33–63.
- MORAN, R. C. 1986. The neotropical fern genus *Olfersia*. Amer. Fern J. 76: 161–178.
- . 1987. Monograph of the neotropical fern genus *Polybotrya* (Dryopteridaceae). Bull. Illinois Nat. Hist. Surv. 34: 1–138.
- PLATNICK, N. I. 1989. An empirical comparison of microcomputer parsimony programs, II. Cladistics 5: 145–161.
- PROCTOR, G. R. 1977. Pteridophyta. In: R. A. Howard (editor), Flora of the Lesser Antilles 2: 1–414.
- RADDI, G. 1825. Plantarum brasiliensium nova genera et species. Pars. 1. Tipographia Aloisii Pezzati, Florence.
- SEHNEM, A. 1979. Aspidiaceae. In: R. Reitz (editor), Flora Illustrada Catarinense, I ASPI. 1: 1–356.
- SMITH, A. R. 1986. Revision of the neotropical fern genus *Cyclodium*. Amer. Fern J. 76: 56–98.
- SODIRO, A. 1883. Recensio cryptogammarum vascularum provinciae Quitensis. Quito.
- . 1893. Cryptogammae vasculares Quitensis. Quito.
- TRYON, R. M. 1972. Endemic areas and geographic speciation in tropical American ferns. Biotropica 4: 121–131.

- & A. F. TRYON. 1982. Ferns and Allied Plants with Special Reference to Tropical America. Springer-Verlag, New York.
- WALKER, T. G. 1966. A cytotaxonomic survey of the pteridophytes of Jamaica. *Trans. Roy. Soc. Edinburgh* 66: 169–237.
- WIDÉN, C.-J., J. SARVELA & D. M. BRITTON. 1983. On the location and distribution of phloroglucinols (filicin) in ferns. *Ann. Bot. Fenn.* 20: 407–417.

INDEX TO COLLECTORS' NUMBERS

This monograph is based on the specimens cited below, which consist of about 1,500 herbarium sheets from approximately 530 collections in 25 herbaria (see acknowledgments for the list of herbaria). Types are in boldface. The abbreviations in parentheses refer to the following species of *Stigmatopteris*, which are arranged alphabetically in the taxonomic treatment.

brev = *brevinervis*; bulb = *bulbifera*; caud = *caudata*; chim = *chimalapensis*; cont = *contracta*; gemm = *gemmipara*; hemip = *hemiptera*; het = *heterocarpa*; hp = *heterophlebia*; ic = *ichthiosma*; jam = *jamaicensis*; kil = *killipiana*; lech = *lechleri*; long = *longicaudata*; mi = *michaelis*; ne = *nephrodioides*; opaca = *opaca*; pp = *pellucidopunctata*; pri = *prionites*; pter = *pterorhachis*; ro = *rotundata*; sord = *sordida*; tyu = *tyucana*.

Aguilar 861 (long); 865 (long); 927 (pp). Allard 22558 (long). Alston 494 (ro); 8744 (sord); 8745 (hp); 8803 (kil); 8848 (kil). Alston & Lutz 289 (caud). Antonio 2050 (hp). Armond 557 (kil). Aymard et al. 3747 (lech).

Baker 5934 (hp). Barringer & Gómez-Laurito 2583 (hp). Barrington 410 (long). Beck 1625 (long); 8500 (pp). Belanger 821 (ro). Bernardi 938 (ro). Blanchet 2483 (tyu, pri). Bohs et al. 1704 (long). Box 1966 (ro). Brade 5892 (tyu); **8231** (het); **8250** (brev); 8340 (brev); 8343 (brev); 8473 (het); 8474 (het); 8476 (het); 8478 (caud); 8510 (het); 9972 (tyu); 9977 (tyu); 18228 (caud); 18405 (pri). Brade & Brade **353** (sord); **497** (long). Brant et al. 1679 (pp). Breedlove 35028 (long); 35128 (long); 56494 (long). Breedlove & Smith 32672 (long). Britton et al. 1361 (ro); 2250 (ro); Broadway 5355 (ro); 6123 (ro). Buchtien 64 (long); 233 (long); 2166 (long). Burger & Antonio 11179 (sord). Burger & Liesner 6773 (long). Burger & Stolze 5055 (sord); 5057 (sord). Burger et al. 10735 (cont).

Calzada 5212 (long). Cardénas 1020 (long). Cazelet & Pennington 5276 (ic). Chacón 319 (sord); 852 (long); 1776 (hp). Chacón & Herrera 1624 (hp). Checkley 7 (ro). Chrysler 4777 (jam). Churchill 5255 (hp). Churchill et al. 4089 (sord); 4549 (hp); 5984 (long). Claros 73 (sord). Clausen 133 (caud). Clement 633 (hemip); 674 (hemip); 945 (hemip); 949 (hemip); 961 (hemip). Conant 792 (long). Cooley 8325 (ro). Cornman 914 (cont); 1091 (cont); 1180 (hp); 1210 (hp); 1284 (hp). Cremers 9113 (ro); 9140 (ro). Croat 22998 (long); 25818 (long); 27477 (hp); 27541 (long); 27736 (long); 36176 (long); 37492 (long); 43598 (sord); 48097 (long); 49916 (hp); 54475 (ne); 60576 (ne); 60765 (ne); 66559 (hp); 68108 (caud); 68154 (sord); 68882 (kil); 69108 (long); 69137 (hp); 70911 (bulb). Croat & Grayum 60043 (hp); 60177 (long); 60215 (long); 60216 (hp); 60217 (hp). Croat & Liesner 1010 (hp). Crosby et al. 521 (jam). Cuatrecasas 15122 (long); 15240 (long); 17336 (hp).

de Granville 1291 (long); 1434 (long); 8873 (ro). de

la Sota 5238 (cont). Dombrowski & Saito 1232 (caud). Dryer 366 (long); 396 (hp). Dusén 725a (brev); 2538 (caud); 10244 (het); 10341 (caud); 13727 (brev); 14115 (het); 14680 (het); 14687 (caud). Duss 80 (ro); 729 (ro); 1561 (ro); 4074 (ro).

Eggers 905 (ro); 6164 (ro); 6869 (ro). Ekman 5268 (gemm); 7424 (gemm); 10113 (gemm); 14356 (hemip). Elias 8 (pp). Evoy 44 (kil). Ewan 16775 (hp).

Fendler **98** (ro); 198 (ne). Finch 169 (long). Forero et al. 2309 (hp); 7407 (hp); 8793 (het). Foster P-84-91 (long). Foster & Wachter 7437 (pp). Foster et al. 10908 (long). Franco et al. 1148 (kil). Funck & Schlim 411 (ne).

Gardner 131 (caud). Glaziou **964** (tyu); 2396 (caud); **2400** (het, brev, pri); **2401** (het); 3333 (brev); 6414 (caud); 7245 (tyu). Glocker 32 (pri). Gómez 281 (cont); 987 (hp); 1133 (cont); 2182 (long); 2330 (cont); 3522 (hp); 18641 (sord); 18778 (long); 19288 (hp). Gómez & Wagner 6856 (long); 79027 (cont). Gómez et al. 19173 (hp); 20858 (hp). Gómez-Pompa et al. 5457 (long). González 14 (long). Grayum 2641 (sord); 4570 (cont); 5374 (cont); 6651 (hp); 6893 (long). Grayum & Jacobs 3598 (sord). Grayum & Schatz 3089 (long). Grayum & Sleeper 3683 (long); 3714 (cont). Grayum & Zamora 9375 (kil); 9376 (sord). Grayum et al. 3288 (hp); 5043 (hp); 5495 (kil); 7910 (long); 7922 (lech). Grijalva 290 (sord). Guzmán-Valdez 892 (long).

Haerchen 106 (het). Hagemann & Leist 2072 (bulb). Hahn 37 (ro); 352 (long). Hallberg 1724 (long). Hammel 2227 (hp); 4858 (kil); 11495 (sord); 12382 (sord). Hammel & de Nevers 13578 (hp). Hammel & Kress 13398 (mi). Hammel & Zuchowski 13880 (hp). Hammel et al. 14238 (long); 14827 (kil). Harling et al. 19737 (opaca). Harris 7277 (jam); 7419 (jam). Harrison **59** (hp). Hart 200 (jam); 337 (ro); **1236** (ro); **3707** (ro); **6259** (ro). Hatch & Wilson 346 (sord). Hatschbach 10748 (het); 22873 (caud); 24376 (het); 24739 (caud); 25939 (het); 41955 (het). Hatschbach & Scherer 26665 (caud). Haught 1931 (pp). Hazlett 3029 (long). Heinrichs 550 (bulb). Hellwig 491 (long); 492 (long); 494 (long). Hernández **1282** (chim). Herrera Ch. et al. 162 (hp); 316 (hp); 336 (cont); 2175 (sord); 2980 (lech). Hioran & Clement 6442 (hemip). Hodge 103 (ro); 104 (ro); 2377 (ro). Hodge & Hodge 1972 (ro). Holm-Nielsen & Jeppesen 811 (hp); 992 (opaca). Holm-Nielsen et al. 2906 (opaca); 24819 (ic). Hoover et al. 4304 (hp); 4325 (hp).

Imray 17 (ro); 39 (ro).

Jansson 740a (caud). Jenman 60 (jam). João & Rohr 392 (het). Johnston 303 (ro).

Kalbreyer **1807** (mi). Karsten **9** (ne). Kenoyer 34 (sord). Killip 2919 (kil); 5159 (cont); 5344 (long); 5387 (hp); 5444 (long); 12147 (kil). Killip & Smith 23906 (long); 28984 (hp). Kirkbride 2377 (pter). Krueger 17107 (pri). Kummrow & Hatschbach 2536 (het).

Laegaard 52431 (long); 51610 (sord); 51611 (hp); 51614 (opaca); 52224 (mi). Lancaster 836 (cont); 893 (hp). Lechler **2497** (lech). Le Gallos 2965 (ro). Lehmann 8951 (hp). Lellinger 362 (ro); 367 (ro); 507 (ro). Lellinger & de la Sota **194** (kil). Lellinger & White 1412 (hp); 1428 (sord); 1476 (hp). Leprieur 270 (ro). León, B. et al. 311 (pp). León, Fre. et al. 10311 (hemip); 10409 (hemip); 10486 (hemip); 11133 (hemip). L'Herminier 115 (ro). Liebmann **737** (long); **738** (long); **739** (long); **2694** (long). Linden 1683 (jam). Liesner & Holst 21882 (long). Liesner & Medina 13739 (ne). Liesner & Stannard 16909 (long). Lloyd 902 (ro). Luederwaldt 21149 (tyu); 21821 (caud). Luschnath 120 (pri).

MacDougal et al. 3811 (long). Madison et al. 3472 (lech). Maguire et al. 36864 (long). Marie 516 (ro). Martius **305** (pri). Maxon 790 (jam); 1071 (jam); **1738** (jam); 2388 (jam); 5647 (long); 8898 (jam); 8863 (jam); 9158 (jam); 9307 (jam). Maxon & Harvey 8075 (long). Maxon & Killip 7 (jam); 169 (jam); 716 (jam). McAlpin 1043 (long); 1313 (hp); 1326 (hp); 1396 (kil). McCallum 104 (ro). McDonough et al. 371 (mi). McPherson 6774 (hp); 8885 (long); 9730 (hp); 12035 (long); 12310E (long); 12677 (hp). Mendonca 1355 (caud). Mexia 4893-a (pri); 5492 (pri). Mickel 484 (long); 975 (long); 990 (long); 1523 (long); 2241 (cont); 2249 (cont); 2622 (hp); 2955 (hp); 3283 (sord); 3430 (cont); 3447 (hp); 5662 (long); 6369 (long); 6392 (long); 6403 (sord); 9412 (ro). Mickel & Pardue 6543 (long); 6727 (long). Molina R. et al. 17321 (sord). Moran 3165 (hp); 3166 (cont); 3187 (cont); 3188 (hp); 3206 (long); 3315 (sord); 3330 (cont); 3545 (ic); 3562 (kil); 3576 (opaca); 3582 (lech); 3607 (sord); 3611 (kil); 3613 (hp); 3624 (pp); 3696 (lech); 4048 (long); 4130 (hp); 5119 (lech); 5250 (ic). Morton 5373 (ro); 6184 (ro); 9569 (hemip). Mosén 2694 (caud). Moya 0011 (lech). Müller 1038 (brev).

Nee & Schatz 19868 (long). Nee et al. 26382 (long). Neill 1886 (hp); 3826 (hp). Nisman S. **98** (cont).

Ocampo S. 1029 (hp); 1771 (sord). Oliveira & Cordeiro 909 (het). Øllgaard et al. 35212 (pp); 35859 (opaca); **35866** (bulb); 39229 (hp); 57515 (long); 90435 (opaca). Ortega & González 369 (ne). Ortega et al. 1822 (pter).

Pabst 799 (het). Palacios 4030 (lech). Perkins 1161 (jam); 1613 (jam). Pittier 12172 (ne). Prestoe 214 (ro). Proctor 4257 (gemm); 17244 (ro); 20345 (ro); 32327 (hp); 38712 (opaca). Purpus 7256 (sord).

Questal 2905 (ro).

Ravins 961 (hemip). Regnell 254a (caud); 358 (caud). Reitz C205 (caud); C206 (brev); 227 (caud); 276 (brev); C919 (het); 1909 (caud); 3141 (het); 3542 (cuad). Reitz & Klein 3068 (het); 3077 (caud). Rivero et al. 1602 (pter). Rohr 352 (brev); 392 (het); 1006 (het); 1072 (caud). Roviroso 822 (long).

Scamman 7667 (hp). Schenck 494 (het); 794 (pri). Schlim 596 (pter); 856 (pter); **1683** (= pp, but syntype of cont). Schmalz 106 (het); 191 (caud). Sehnem 808 (het); 3086 (het). Sieber **350** (ro). Skutch 145 (jam). Smith, A. R. 1031 (pter); 1692 (hp); 2121 (hp). Smith, A. R. et al. 1678 (long); 1813 (sord); 1862 (cont); 1876 (hp); 2194 (long); 2235 (hp); 2247 (cont). Smith, H. H. **1045** (pter). Smith, H. H. & G. W. Smith 659 (ro). Smith, L. B. 1391 (caud). Smith, L. B. & Reitz 6127 (het). Sodiro 48/1 (ic); **54/2** (opaca); **54/3** (opaca); **2615** (mi). Soejarto & Villa 2685 (sord). Solomon 18469 (long). Spannagel 332 (het). Spruce 4012 (long); **4653** (opaca); **4719** (lech); **4720** (pp); 5714 (ic). Standley 37169 (hp); 37834 (cont). Standley & Torres R. 51061 (cont); 51069 (hp). Stehlé 1104 (ro); 1463 (ro); 1887 (ro); 3303 (ro); 4807 (ro); 4883 (ro); 6725 (ro); 7238 (ro); 8436 (ro). Steyermark 61403 (ne); 89747 (ne). Steyermark & Espinoza 111174 (ne); 111493 (ne). Steyermark & Nevling 95914 (ne). Steyermark & Nilsson 314 (ro). Steyermark & Rabe 96115 (ro). Steyermark & Steyermark 95406 (long); 95406-A (ne). Steyermark & Stoddart 118173-A (ne). Steyermark et al. 48744 (long); 51710 (long); 110227 (pter); 125086 (ne). Stolze 1487 (long); 1634 (hp). Stork 2263 (cont); 2658 (cont); 2722 (hp). Stübel 797 (ic).

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(jam). Ule 68 (caud); **70** (caud & ulei); 187 (het). U.S. Expl. Exped. 23 (caud).

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Wacket 50 (tyu); 286 (caud); 21149 (tyu). Wagner **460** (pter); 1402 (het). Wagner & Gómez 79021a (hp). Wachter et al. 200 (long). Watt 82 (jam). Webster 13329 (ro); 13566 (ro); 13588 (ro). White & Lucansky 1968150 (cont); 1968174 (cont). Wilbur 7882 (ro). Wilbur & Stone 8919 (long). Wilson & Murray 563 (jam). Wright **1053** (hemip). Wurdack 2002 (pp).

Zak & Espinoza 5287 (opaca). Zak & Jaramillo 3635 (lech).

INDEX TO NAMES

Accepted names are set in roman type; new taxa and combinations appear in boldface; all other names are italicized. In parentheses following an italicized name is the accepted taxon.

Aspidium Sw.

brachyneuron Fée (tyucana)

caudatum

var. *contractum* Christ (contracta)

imrayanum (Hook.) Fée (rotundata)

rotundatum Willd. (rotundata)

Cystopteris Bernh.

jamaicensis Desv. (jamaicensis)

Dryopteris Adans.

subg. *Stigmatopteris* (C. Chr.) C. Chr. (= *Stigmatopteris*) group *Peltochlaena* Fée ex C. Chr. excluded

carrii (Baker) C. Chr. (heterocarpa)

caudata (Raddi) C. Chr. (caudata)

christii C. Chr. (opaca)

coalescens (Baker) C. Chr. (opaca)

cyclocolpa (Christ) C. Chr. (lechleri)

imrayana (Hook.) Domin (rotundata)

longicaudata (Liebm.) Maxon (longicaudata)

pellucidopunctata C. Chr. (pellucidopunctata)

prionites (Kunze) C. Chr. (prioniodes)

gemmipara (C. Chr.) Maxon ex Proctor (gemmipara)

hemiptera (Maxon) C. Chr. (hemiptera)

heterophlebia (Baker) C. Chr. (heterophlebia)

ichthiosma (Sodiro) C. Chr. (ichthiosma)

longipetiolata C. Chr. (ichthiosma)

nothochlaena Maxon (jamaicensis)

paucinervata C. Chr. (opaca)

prasina (Baker) C. Chr. (lechleri)

rotundata C. Chr. (rotundata)

sordida Maxon (sordida)

sylicola (Baker) C. Chr. (michaelis)

tijuccana C. Chr. (tyucana)

ulei (Christ) C. Chr. (ulei)

Meniscium Schreber

opacum Baker (opaca)

Nephrodium Michaux

imrayanum Hook. (rotundata)

Phegopteris Fée

brevinervis Fée (brevinervis)

flavopunctata (Kaulf.) Fée (rotundata)

- denticulata* Fée (prionites)
heterocarpa Fée (heterocarpa)
lechleri Mett. (lechleri)
macrophylla (Hook.) J. Smith (pellucidopunctata)
oligophlebia Salmon (opaca)
opaca (Baker) Christ (opaca)
perforata Fée uncertain
tenuis Fée (tyucana)
ulei Christ (ulei)
- Polypodium L.
- alloëpteron* Kunze uncertain
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caudatum Raddi (caudata)
caudatum Kaulf. (caudata)
coalescens Baker (opaca)
cyclocolpon Christ (lechleri)
dentatum Baker (ichthiosma)
flavopunctatum Kaulf. (rotundata)
heterophlebium Baker (heterophlebia)
ichthiosmum Sodiro (ichthiosma)
longicaudatum Liebm. (longicaudata)
macrophyllum Hook. (pellucidopunctata)
michaelis Baker (michaelis)
nephrodioides Klotzsch (nephrodioides)
oligophlebium Baker in Hook. & Baker (opaca)
prasinum Baker (lechleri)
prionites Kunze (prionites)
punctatum Spruce in Hook. (lechleri)
sylvicolum Baker (michaelis)
tyucanum Raddi (tyucana)
- Stigmatopteris C. Chr.
- alloëptera* (Kunze) C. Chr. uncertain
bradei Rosenstock (brevinervis)
brevinervis (Fée) R. C. Moran
bulbifera R. C. Moran
carrii (Baker) C. Chr. (heterocarpa)
caudata (Raddi) C. Chr.
- chimalapensis* Mickel & Beitel
clypeata (Maxon & C. Morton) Lellinger excluded
contracta (Christ) C. Chr.
cyclocolpa (Christ) C. Chr. (lechleri)
ecuadorensis C. Chr. (lechleri)
gemmaipara C. Chr.
guianensis (Klotzsch) C. Chr. excluded
hemiptera (Maxon) C. Chr.
heterocarpa (Fée) Rosenstock
 var. *basilaris* Rosenstock (heterocarpa)
heterophlebia (Baker) R. C. Moran
ichthiosma (Sodiro) C. Chr.
jamaicensis (Desv.) Proctor
killipiana Lellinger
lechleri (Mett.) C. Chr.
litoralis Rosenstock (sordida)
longicaudata Liebm.
meniscioides Kramer in Kramer & van Donselaar
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michaelis (Baker) C. Chr.
nephrodioides (Klotzsch) C. Chr.
nothochlaena (Maxon) C. Chr. (jamaicensis)
opaca (Baker) C. Chr.
palmensis Rosenstock (longicaudata)
paludosa (C. Morton) R. Tryon & A. Tryon excluded
pellucidopunctata (C. Chr.) C. Chr.
prasina (Baker) C. Chr. (lechleri)
prionites (Kunze) C. Chr.
 var. *denticulata* (Fée) C. Chr. (prionites)
- pterorhachis** R. C. Moran
- rotundata* (Willd.) C. Chr.
 var. *trinidadensis* C. Chr. (rotundata)
sancti-gabrielii (Hook.) C. Chr. excluded
sordida (Maxon) C. Chr.
tyucana (Raddi) C. Chr.
ulei (Christ) Sehnem
varians (Fée) Alston excluded